SEASONAL VARIATION IN QUALITY AND SURVIVAL OF NESTLING TREE SWALLOWS (*TACHYCINETA BICOLOR*): TESTS OF ALTERNATE HYPOTHESES

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By

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DEDICATION

This thesis is dedicated to my partner in life, Chris, and our extraordinary daughters, Isla Brooke and Cleo Talise. Chris, words cannot express my gratitude for your patience and boundless encouragement, thank you for supporting me on my chosen path to becoming "Real." Isla and Cleo, you help me keep life in perspective and bring me so much joy, I love you to the moon and back.

"Real isn't how you are made. It's a thing that happens to you. It doesn't happen all at once. You become. Generally, by the time you are Real, most of your hair has been loved off, and your eyes drop out and you get loose in the joints and very shabby." – Margery Williams from "The Velveteen Rabbit"

ABSTRACT

Understanding the patterns and processes that create differences among individuals in components of fitness, like the probability of survival or reproductive rates, is essential to our knowledge of population dynamics and for informing conservation efforts. For organisms in seasonal environments, early-breeding individuals regularly attain higher fitness than their late-breeding counterparts. Two primary hypotheses, related to quality and date, have been proposed to explain lower reproductive success of late breeders, but the veracity of these ideas has not been fully resolved. I tested predictions associated with these hypotheses to assess the effects of indices of parental and environmental quality on nestling quality and survival in an insectivorous passerine, the tree swallow (*Tachycineta bicolor*), at two widely separated breeding locations in western Canada.

I combined experiments and statistical modelling of observational data to evaluate two mechanisms proposed to contribute to seasonal decline in environmental quality: an increase in nest parasite abundance and a decrease in food abundance with later breeding dates. A parasite reduction experiment revealed a disproportionate benefit of parasite removal on length of primary feather for early-hatched nestlings, suggesting greater energetic constraints early in the breeding season. Furthermore, late-hatched nestlings from parasite-reduced nests had longer head-bill lengths than their control counterparts, and developed head-bills of similar length to those of early-hatched nestlings. Other than these findings, there were few detectable effects of parasites on nestling size, growth and immunity, as has been reported from several previous studies. Indeed, negative effects of parasites were only apparent when food (i.e., insect) biomass was considered. In a second series of experiments in which parental quality was controlled, I also tested whether food abundance declined during the breeding season, as predicted if environmental conditions deteriorate seasonally (i.e., date). Reduced reproductive success of late-breeding individuals was causally related to a seasonal decline in environmental quality. Declining insect biomass and enlarged brood sizes resulted in nestlings that were lighter, in poorer body condition, had shorter head-bills, shorter and slower growing ninth primary feathers and that were less likely to survive to fledge. Next, I asked whether results obtained from long-term mark-recapture data corroborated findings of short-term manipulations.

I examined seasonal variation in first-year apparent survival to investigate the relative influence of large-, small- and individual-scale factors associated with the quality and date hypotheses. Although parental quality was an important predictor of first-year apparent survival of tree swallows, my results further suggested that quality of parents was not the primary factor influencing seasonal variation in first-year apparent survival. Rather, findings were most consistent with the date hypothesis. The relationship between apparent survival and a direct measurement of environmental quality indicated that annual variation in moisture had important consequences for first-year apparent survival of tree swallows in Saskatchewan. First-year apparent survival probabilities were higher during wet years and wetter conditions are generally linked to greater insect abundance. In British Columbia, nestlings from larger broods were less likely to survive, possibly as a result of receiving less food. Apparent survival probabilities were also higher when food was more abundant.

I demonstrated that both parental and environmental quality influenced seasonal variation in fitness-related traits of tree swallows. However, the strongest evidence suggests that environmental quality, and in particular food abundance, had the greatest effect on seasonal variation in nestling quality, reproductive success and first-year apparent survival in tree swallows. My results highlight the importance of considering regional precipitation trends when projecting effects of climate change on demography of aerial insectivores.

ORGANIZATION OF THESIS

There will be some redundancy in the introduction and methods of each data chapter of my thesis because data chapters were written in the format of independent manuscripts for publication in peer-reviewed journals. I took the lead role in designing experiments, analyzing data and writing papers. Although I use the pronoun “I” throughout, I would like to acknowledge the contributions of co-authors and reviewers. Chapter 2 was reprinted from: Harriman, V.B., Dawson, R.D., Clark, R.G., Fairhurst, G.D., Bortolotti, G.R., 2014. Effects of ectoparasites on seasonal variation in quality of

nestling Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 92: 87-96, with permission from NRC Research Press.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. GENERAL INTRODUCTION: SEASONAL VARIATION IN AVIAN FITNESS

A principal goal in evolutionary ecology is to determine why some individuals attain higher fitness than others. Understanding the patterns and processes driving differential fitness among individuals is essential to our knowledge of population dynamics and for informing conservation efforts. Variability in how organisms respond to and interact with their environment ultimately produces variation in fitness among individuals. One key decision individuals in all environments must make is when to reproduce, a decision based on trade-offs involving a variety of factors including environmental cues and physiological condition. For organisms in seasonal environments, timing of reproduction is a critical factor influencing components of fitness. Early-breeding individuals regularly attain higher fitness, like survival or reproductive rates, than do their late-breeding counterparts (e.g., Kelly and Levin 2000, Varpe et al. 2007, Uller and Olsson 2010).

1.1 TIMING OF BREEDING AND FITNESS

Two primary hypotheses have been proposed to explain lower reproductive success of late breeders, but the veracity of these ideas has not been fully resolved. The 'quality' hypothesis predicts that higher quality individuals (phenotypic quality or condition) breed earlier in the season and that declining reproductive success among late breeders is a consequence of the lower quality territories of late breeders or poor performance by late-breeding individuals of low quality (Price et al. 1988, Verhulst and Tinbergen 1991). Alternately, the 'date' hypothesis purports that environmental quality declines seasonally and that the observed pattern in reproductive success is causally related to timing of breeding and thus affects all individuals in the same way (Perrins 1970). The two hypotheses are not mutually exclusive, and their effects may be manifested simultaneously, at different times throughout the breeding season or at different life-history stages (Verhulst et al. 1995, Grüebler and Naef-Daenzer 2010, Gurney et al. 2012).

The trend of declining reproductive success with later breeding dates has been extensively studied in avian populations (reviews in: Arnold et al. 2004, Verhulst and Nilsson 2008). Aspects of both parental and environmental quality have important consequences for components of fitness in birds. Verhulst and Nilsson (2008) suggest that the value of timing studies is to identify when aspects associated with environmental quality influence reproductive success and to identify the mechanism(s) mediating a seasonal deterioration in environmental quality. Knowledge of these relationships is particularly important in making predictions about environmental effects on avian populations under changing climatic conditions (Lyon et al. 2008, Verhulst and Nilsson 2008) and substantiation of purported mechanisms is essential.

1.2 FOCAL SPECIES: TREE SWALLOW (*TACHYCINETA BICOLOR*)

Tree swallows are aerial insectivores, a guild of birds experiencing population declines in many areas of North America (Nebel et al. 2010, Shutler et al. 2012). Multiple potential causes have been proposed for population declines, including a mismatch between timing of breeding and food availability and declines in habitat quality and food availability (Nebel et al. 2010). Tree swallows breed throughout southern Canada and the northern United States and generally winter in the southern United States and Mexico. They are secondary cavity nesters and will readily accept nest boxes. Tree swallows generally arrive on the breeding grounds by mid-April, lay ~6 eggs in early-mid May (Winkler et al. 2011, Chapter 4) and eggs hatch in June after ~13-14 days of incubation (Ardia et al. 2006a). Tree swallow nestlings spend ~18-22 days in the nest (Stephenson et al. 2009).

Parents were captured at the box using swing-door trapping methods in which birds were immediately measured and released (PG) or held for 30 minutes or until the other parent was also captured, whichever was shorter (SDNRA). Female and male tree swallows are generally distinguished from one another using breeding morphology (cloacal protuberance in males, brood patch in females). Male swallows obtain adult plumage within their first year of life. Females have plumage that is completely or

partially brown when entering their second year (SY) of life, thus allowing SY females to be distinguished from older after-second year (ASY) females (Hussell 1983).

1.3 STUDY AREAS

All research was conducted at two study areas in western Canada (Fig. 1.1), at the St. Denis National Research Area (52°N, 106°W) and near Prince George, British Columbia (53°N, 122°W). Specific details of study sites are described in each chapter.

Fig. 1.1 Locations of study areas, Prince George, British Columbia (circle), and St. Denis National Research Area, Saskatchewan (triangle).

1.4 THESIS OBJECTIVES

My broad goal was to test predictions associated with the quality and date hypotheses by evaluating the relative and interactive effects of quality and date-

associated indices on nestling quality and survival in an insectivorous passerine. I specifically tested the role of ectoparasites (Chapter 2) and food abundance (Chapter 3) as mechanisms driving seasonal decline in environmental quality. I also investigated the effects of indices of parental and environmental quality on first-year apparent survival of tree swallows (Chapter 4).

1.4.1 Seasonal patterns in ectoparasite abundance on offspring quality

A seasonal increase in parasitism may contribute to the declining quality and survival of nestlings hatched later in the season (Verhulst and Nilsson 2008). Populations of avian parasites generally increase as the breeding season progresses (Burtt et al. 1991, Merino and Potti 1995) so late-hatched offspring may face greater parasite challenges than early-hatched individuals due to seasonal changes in parasite abundance. In Chapter 2, I examined the effect of ectoparasites on seasonal variation in nestling quality by comparing characteristics of nestlings raised in control nests to those where nest parasites were removed using an insecticide. Specifically, I tested whether experimental reductions in blow flies and fleas in nests would result in better quality nestlings and, if so, whether benefits of parasite reduction increased seasonally (Fig. 1.2).

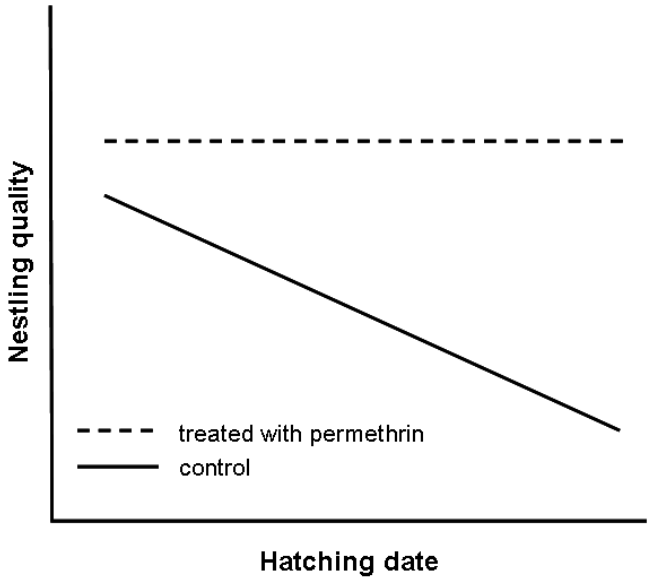


Fig. 1.2 Predicted relationship between nestling quality and hatching date in response to treatment with an insecticide (permethin).

1.4.2 Seasonal patterns in food availability on offspring quality

Food availability is often proposed as the most important factor influencing seasonal variation in reproductive success of many avian species (Perrins 1970, Siikamäki 1998, Verboven et al. 2001). While several studies have documented consequences of seasonally declining food resources on reproductive success (Verboven et al. 2001, Hipfner et al. 2010, Burger et al. 2012), there are few examples of experimental tests for which parental quality is accounted for while simultaneously altering food availability. I conducted a series of manipulations to test predictions associated with the date hypothesis, while accounting for parental quality (Chapter 3). To account for potential effects of parental quality, I paired nests by clutch initiation date and delayed the hatching of one nest within the pair. Subsequently, brood size manipulations were conducted to mimic changes in per capita food abundance (Shutler et al. 2006, Bortolotti et al. 2011). If declining reproductive success with later breeding dates was partly attributed to seasonally-declining food abundance, I predicted that (i) nestlings in enlarged broods (i.e., with reduced food per capita) would be of lower quality and less likely to survive to fledging or return in subsequent years than their control counterparts and (ii) this relationship would be more pronounced later in the season regardless of when parents initiated nests (Fig. 1.3).

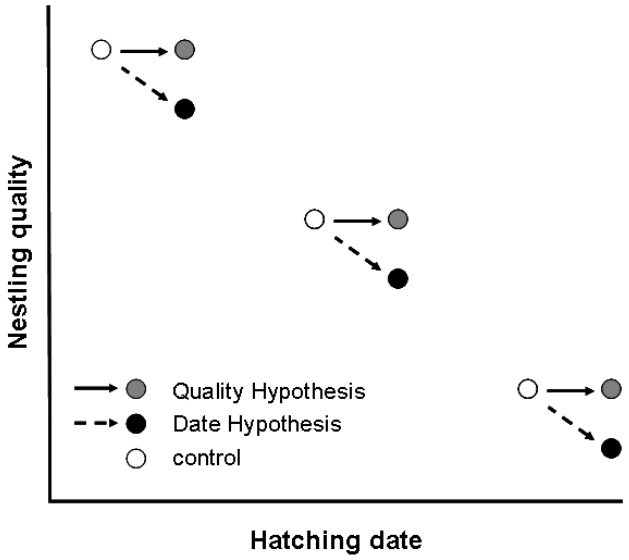


Fig. 1.3 Relationships between nestling quality and hatching date in response to delay treatment as predicted by either the quality or date hypothesis.

1.4.3 Parental and environmental quality effects on apparent survival of offspring

A recent study suggests that declines in recruitment of offspring is the greatest contributing factor to lower fitness of late breeders (Öberg et al. 2013), yet comprehensive investigations of potential drivers of variation in first-year apparent survival probabilities (and thus accounting for recapture probability) of avian offspring are lacking (but see Brinkhof et al. 1997). Variation in demographic rates is likely linked to both large-scale processes affecting most individuals in a population and local-scale factors influencing individual life-histories (Coulson et al. 2001, Reid et al. 2008). Furthermore, large-, small- and individual-scale effects should be considered simultaneously, although this has been generally rare due to the lack of availability of individual-scale information in long-term data sets (Reid et al. 2008). I examined seasonal variation in first-year apparent survival of tree swallows using mark-recapture data (1991-2010 at SDNRA and 2001-2010 at PG; Chapter 4). Specifically, I investigated the relative influence of large-, local- and individual- scale factors associated with the quality and date hypotheses on offspring survival. Four covariates were used to index parental quality: female minimum age, prior breeding site experience of female parents, clutch size and female body mass. Three categories of covariates were considered as indices of environmental quality: large-scale climate factors, and local indices of moisture and wetland depth.

CHAPTER 2: EFFECTS OF ECTOPARASITES ON SEASONAL VARIATION IN QUALITY OF NESTLING TREE SWALLOWS (*TACHYCINETA BICOLOR*)

2.1 INTRODUCTION

In many avian species, quality and survival of offspring declines with later breeding dates (Perrins 1970, Shutler et al. 2006, Verhulst and Nilsson 2008). Two general hypotheses have been proposed to explain this pattern. The quality hypothesis predicts that higher quality individuals (phenotypic quality or condition) breed earlier in the season and the seasonal trend results from poor performance by late-breeding, lower

quality individuals (Price et al. 1988, Verhulst and Tinbergen 1991). The date hypothesis proposes that environmental quality declines seasonally and that the observed pattern in nestling quality is causally related to timing of breeding (Perrins 1970). Thus, the date hypothesis asserts that the decline in environmental quality affects all individuals in the same way. Support for the date hypothesis is frequently reported (Verhulst and Tinbergen 1991, Barba et al. 1995, Siikamäki 1998, Dubiec and Cichoń 2005), yet mechanisms contributing to a seasonal deterioration in the environment remain uncertain. Although food resources have often been cited as a primary cause of this pattern (Perrins 1965, Brinkhof and Cavé 1997, Siikamäki 1998), other mechanisms have also been proposed. For example, a seasonal increase in parasitism may contribute to the declining quality and survival of nestlings hatched later in the season (Verhulst and Nilsson 2008). Populations of avian parasites generally increase as the breeding season progresses (Burtt et al. 1991, Merino and Potti 1995) so late-hatched offspring may face greater parasite challenges than early-hatched individuals due to seasonal changes in parasite abundance.

I examined the effect of ectoparasites on seasonal variation in nestling quality in a migratory songbird, the tree swallow (*Tachycineta bicolor*), by comparing characteristics of nestlings raised in control nests to those where nest parasites were removed using an insecticide (Allander 1997, de Lope et al. 1998). Work was conducted on two widely separated sites with distinct environmental conditions. Specifically, I tested whether experimental reductions in blow flies and fleas in nests would produce larger, faster growing nestlings and, if so, whether benefits of parasite reduction increased seasonally. The date and parental quality hypotheses are not mutually exclusive. These data provided the opportunity to not only test a possible mechanism associated with the date hypothesis, but to examine potential interactive effects of environmental and parental quality on avian fitness components.

I also investigated nestling physiological responses to nest parasites using levels of glucocorticoids. Exposure of birds to stressors, including parasite infestations, generally results in increased secretion of corticosterone (CORT) (Romero 2004, Boughton et al. 2006, Garvin and Schoech 2006), the primary avian glucocorticoid, which has been interpreted as parasites causing an increase in energy expenditure (Raouf et al. 2006, Lobato et al. 2008). Instead of using blood samples, I analyzed levels of

CORT in nestling feathers ($CORT_f$). $CORT_f$ values are related to plasma levels of CORT when the later levels are high, and provide an integrated measurement over the period of feather growth (Bortolotti et al. 2008, Lattin et al. 2011, Fairhurst et al. 2013). Importantly, $CORT_f$ can reveal variation in how individuals cope with parasites (Bortolotti et al. 2009*b*). I predicted that individuals from nests where parasites had been removed would have lower levels of $CORT_f$ compared to nestlings from control nests.

A seasonal decline in nestling quality could be related to a seasonal increase in nest parasite loads and/or to a reduction in nestlings' abilities to contend with nest parasites. Accordingly, I tested whether parasite loads increased in unmanipulated nests and if nestling immunocompetence decreased with later breeding dates. Because food abundance may mediate the impact of ectoparasites on nestlings (Thomas et al. 2007, Brommer et al. 2011), I also evaluated whether aerial insect biomass and parasite treatment interacted to influence nestling size and condition. Finally, to address whether parental quality differed between sites or varied seasonally within a site I considered the influence of site and hatching date on indices associated with parental quality and/or condition.

2.2 METHODS

2.2.1 Study areas

Research was conducted in 2007 at two widely separated sites within the breeding range of tree swallows in Canada. Swallows on both sites nested in artificial boxes. The site (PG) in British Columbia was in the vicinity of Prince George (53^{o}N, 122^{o}W), and was mostly open agricultural habitat interspersed with small stands of deciduous and coniferous trees. Nest boxes were ~30 m apart and mounted on wooden fence posts. Nest box occupancy was 63% (66 of 104 boxes) in 2007.

The Saskatchewan site (SDNRA) was located on the St. Denis National Research Area (52^{o}N, 106^{o}W), 40 km east of the city of Saskatoon, within an undulating agricultural landscape primarily composed of alfalfa (*Medicago sativa* L.) and brome grass (*Bromus inermis* Leyss) cover, agricultural crops and abundant wetland basins. Nest boxes were arranged in two ways: first, as a continuous series of 115 boxes (placed ~30

m apart) and, second, an additional 60 boxes formed 12 distinct "neighborhoods" of 5 boxes each (30 m spacing). All nest boxes on SDNRA were attached to metal posts 1.5 m above ground with the box entrance facing southeast. Box occupancy was 100% in 2007. In accordance with standard protocols at each site, nest material was removed from boxes annually following fledging.

2.2.2 General methods and nestling measurements

Nest boxes were visited every 2 days beginning in early May until an egg was laid, and thereafter nests were visited daily to determine laying rate and clutch size. When laying was complete at a box, visits ceased until 2 days prior to the estimated date of hatch (12 days after the last egg was laid), after which nests were visited daily to determine date of first nestling emergence, hatching success and brood size. When all viable eggs had hatched, parents were captured at the box and mass (nearest 0.5 g measured with a 60 g spring scale) and length of head-bill (nearest 0.01 mm with digital (PG) and dial (SDNRA) calipers) were recorded. Nestling age was calculated by denoting the first day a nestling was present in the nest as day 0 at PG and one day following the presence of the first nestling (i.e., when the majority of eggs had hatched) as day 0 at SDNRA, resulting in a difference of 1 day in age between PG and SDNRA; therefore, all nestlings in a box were assigned the same age. Individual chicks within a nest were uniquely marked with non-toxic markers and banded with aluminium bands at 16 (PG) or 12 (SDNRA) days of age. Measurements of mass (nearest 0.25 g measured with a 30 g spring scale) and length of the head-bill (nearest 0.01 mm with digital (PG) and dial (SDNRA) calipers) were recorded for each nestling in treatment and control (details below) nests every other day from 4- to 16-days-old. Additionally, the length of the ninth primary feather was measured (nearest 0.5 mm with a ruler) every other day from day 8 to 16. Several back feathers were collected from one middle-ranked nestling per box when they were 16-days-old (SDNRA only) for measurement of $CORT_f$, and nest boxes were checked for fledging success on day 22 when the nesting material was collected to quantify ectoparasite loads (details below).

Cell-mediated immune responses are effective against ectoparasite infestations, such as those by hen fleas (*Ceratophyllus gallinae* (Schrank, 1803)) (Tschirren et al. 2007). T-cell-mediated immune function was assessed for two nestlings per box using phytohemagglutinin (PHA). Nestlings were selected based on their position in the mass hierarchy within a nest (middle two nestlings) on day 9 at PG and day 8 at SDNRA (resulting in injection at the same actual age, see above). I injected 30 µl of 2 mg/ml of PHA in phosphate buffered saline into the right wing web and measured wing web thickness (to the 0.01 mm) with a thickness gauge (nearest 0.01 mm at PG, nearest 0.005 mm at SDNRA) just prior to and 24 hours post injection (Smits et al. 1999). The left wing web was measured to account for growth in web thickness over the 24 hour period. Cell-mediated immune response (CMI) was calculated by determining the difference in web thickness before and after injection and adjusting for growth (O'Brien and Dawson 2008). All measurements were performed by one observer at PG and two observers at SDNRA with the exception of PHA which was performed by only one observer at SDNRA.

2.2.3 Insect sampling

Passive insect samplers (n = 2 at PG, n = 3 at SDNRA) were erected with the opening of the net 2 m above ground. Insects accumulated in jars containing 70% ethanol and jars were collected every ~24 hours (PG) or ~12 hours (SDNRA) and stored in fresh 70% ethanol until processed. After removal of non-insect biomass, samples were placed in a drying oven at 95 °C for 3 hours (or until completely dry) and weighed (nearest 0.00001 g with an analytical balance). Wind speeds were collected at on-site weather stations (one per site) with anemometers placed 3 m (PG) and 10 m (SDNRA) above ground. Insect biomass was corrected for sampling time and mean wind speeds during the sampling period. Insect biomass sampling, processing and corrections were based on Quinney et al. (1986). Mean food biomass was calculated for each nest for the 15 day period when nestlings were 2- to 16-days-old using the corrected daily insect biomass averaged among samplers on each site.

2.2.4 Ectoparasite life-history and removal

Blow flies (Diptera: Calliphoridae) and fleas (Siphonaptera) are common nest parasites of birds (Rothschild and Clay 1952, Bennett and Whitworth 1992) and can negatively affect avian offspring immunocompetence, growth and survival ((blow flies: Merino and Potti 1995, 1998, Saino et al. 1998, Puchala 2004, Simon et al. 2004, O'Brien and Dawson 2008, Streby et al. 2009), (fleas: Fitze et al. 2004, Pitala et al. 2009, Brommer et al. 2011)). Adult blow flies (*Protocalliphora* and *Trypocalliphora* spp.) lay eggs in host nests (Bennett and Whitworth 1991) and the larvae are obligate blood-feeding parasites of nestlings. Most species of blow fly are intermittent feeders, living in the nest material between blood meals, although *Trypocalliphora braueri* spends the entire larval stage subcutaneously (Sabrosky et al. 1989). Bird fleas spend most of their life-cycle in host nesting material rather than on the host and the adult stage of the flea is sanguivorous (Marshall 1981).

Nests were matched by clutch initiation date and randomly assigned to either the control or treatment group. After temporary removal of eggs or nestlings, nests and the entire inside of nest boxes were sprayed with a 0.50% solution of permethrin (treatment) or tap water (control) 2 days before the expected hatching date, and again at 4, 8, 12, and 16 days post-hatch. Permethrin is a synthetic pyrethroid derived from extracts of chrysanthemum flowers. Pyrethrins attack the nervous system of all insects and are effective against larval and adult stages, but not eggs (Edwards 2006), and have successfully been used to decrease parasite loads in nests of passerine species (Allander 1998, Szép and Møller 1999, Christe et al. 2000). In total, 28 and 13 nests (resulting in 151 and 86 nestlings) were treated with permethrin and 27 and 12 nests (resulting in 144 and 77 nestlings) were used as controls at PG and SDNRA, respectively. Nest mites were present at both sites (noted in 1 control box at each site), and feather mites and lice were likely present in small numbers (Shutler et al. 2004), but abundances of mites and lice were not quantified.

2.2.5 Sampling nests for parasites

All manipulated and control nests were collected within 1 week after nestlings fledged to determine parasite burdens in nests as well as the effectiveness of permethrin.

Nests were stored in sealed plastic bags for 14 days at room temperature (Dawson et al. 2005*a*) and subsequently frozen once then heated in an oven for 24 hours at 75 °C (PG), or frozen and thawed twice (SDNRA) to ensure that fleas were killed. Nest material collected from nests at PG (n = 52) and SDNRA (n = 23) was separated to extract all blow fly pupa and puparia. Large materials (grass and feces) were then removed until a fine, homogenous mixture of nest material remained, which was then weighed (nearest 0.01g with a digital scale). A complete sampling of 5 control nests indicated that a reliable estimate of flea numbers could be achieved by subsampling 5 (0.5 g) aliquots of nest material (Harriman et al. unpublished data). Five 0.5 g aliquots were then sampled from the homogenous mixture of nest material for a random sample of nests collected in PG (n = 16) and SDNRA (n = 23) and each aliquot was searched for fleas using a light magnifier. Estimates of fleas in nests were calculated by multiplying the average number of fleas/aliquot found in the five aliquots by the number of aliquots available for sampling/nest (mass of homogenous mixture of nest material/0.5). Abundances of blow flies and fleas were positively correlated with brood size (also see: Hurtrez-Boussès et al. 1999, Dawson et al. 2005a). To account for variation in parasite loads related to brood size, numbers of blow flies and fleas in nests were divided by the number of nestlings at hatch.

2.2.6 Corticosterone extraction

Extraction of CORT from feathers followed Bortolotti et al. (2008) and has been replicated with tree swallows (Harms et al. 2010, Fairhurst et al. 2012b) and other species (Fairhurst et al. 2011, Lattin et al. 2011, Fairhurst et al. 2012a). The calamus of each feather was removed and the length of the remaining feather sample was measured. Each feather was cut into pieces < 5 mm^2 and placed in separate glass vials. Ten mL of methanol (HPLC grade, Fisher Scientific, Fairlawn, New Jersey, USA) was added to samples which were then placed in a sonicating water bath at room temperature for 30 minutes, followed by incubation at 50 °C overnight in a water bath. Vacuum filtration was used to separate the methanol from feather. Methanol extracts were then placed in a 50 °C water bath and evaporated under a fume hood. Dried sample extract residues were

reconstituted in a small volume of phosphate buffered saline (0.05M; pH, 7.6) and subsequently frozen at –20 °C until they were analyzed in duplicate using radioimmunoassay. The efficiency of the methanol recovery was assessed using three additional feather samples each spiked with a small amount (approximately 5000 CPM) of ^{3}H-corticosterone in the extraction. For additional information about extraction validation, see Supplementary Appendix S1 in Bortolotti et al. (2008). Samples were extracted in one batch with 80% of the radioactivity being recoverable from reconstituted samples. Samples were measured in three assays with an average intra-assay coefficient of variation, calculated from three known-concentration standards of 6.9% and an inter-assay coefficient of variation of 15.3%. Assays had a mean limit of detection (80% bound) of 12.9 pg CORT/assay tube. Data are expressed as pg CORT per mm of feather, which gives a valid estimate of CORT per unit time of feather growth (Bortolotti et al. 2008, Bortolotti et al. 2009a).

2.2.7 Statistical analyses

Generalized linear models with normal (blow flies) and negative binomial (fleas) distributions (PROC GENMOD, SAS Institute Inc., Cary, North Carolina, USA) were used to examine the effectiveness of nest parasite treatment and the relationship between site and clutch initiation date (standardized by the first clutch initiation date within each site) on abundance of fleas and blow flies in nests. To investigate potential effects of parasite treatment on nestling growth, growth rate constants were calculated for each nestling. I used a non-linear procedure to fit logistic models (PROC NLIN) for gain of body mass and growth of head-bill using the Levenberg-Marquardt estimation method. For growth of ninth primary feather, I fit a linear model (Dawson et al. 2005*b*). Individuals without complete growth data (days 4 to 16 for mass and head-bill and days 8 to 16 for primary feather) were excluded.

Logistic regressions (PROC GENMOD) were used to consider the effect of treatment, hatching date, insect biomass, brood size and two additive models (treatment + hatching date; treatment + insect biomass) on survival to fledging and subsequent local recruitment of nestlings that fledged. Due to the small numbers of nestlings that either

died prior to fledging or recruited locally, nestling fate and local recruitment were binary responses, i.e., considered by nest rather than by individual. Thus, for each nest, all nestlings fledged or at least one nestling died (fate), and at least one nestling returned to the breeding population as an adult or none returned (recruitment index). The local recruitment index measures return rate and this index should not be considered a surrogate for apparent survival or survival probabilities.

Linear mixed models (PROC MIXED) were used to examine the influence of treatment, hatching date and food abundance (fixed effects) on nestling mass, lengths of the head-bill and primary feather at day 16, growth rates of mass, head-bill and primary feather, and PHA response while accounting for clustering of data within nest boxes by using nest identity as a random factor. Additionally, effects of time of day and nestling mass at injection (fixed effects) on PHA response were considered (Forsman et al. 2010). Preliminary analyses suggested differences among sites. Particularly, mean insect biomass was greater (Fig. 2.1) at SDNRA (mean = 0.621 g, SD = 0.374, n = 25) than PG (mean = 0.102 g, SD = 0.131, n = 26) and decreased (PROC GLM) with hatching date during the nestling period at SDNRA (β = -0.010 ± 0.002, n = 10) but increased with hatching date at PG (β = 0.006 ± 0.001, n = 13). Abundance of blow flies also differed between sites (see results below). Thus, nestling data were analyzed separately by site. Hatching date and insect biomass were correlated and therefore not included simultaneously in the same model. Due to the ecological feasibility of each model, all possible additive combinations of covariates were considered for each dependent variable, including interactions of treatment with hatching date and insect biomass, and an intercept-only (null) model. I considered 8 models at each site for each response variable (10 for PHA response). Parameter estimates (β) were produced using restricted maximum likelihood estimation (REML, PROC MIXED). Although many of these factors (e.g., brood size) may have interacted with measurements of environmental quality such as food abundance, data collected on insect biomass provided context for interpreting results. To investigate seasonal variation in parental quality and condition between sites, I considered the effects of site and hatching date within site on clutch size, brood size, and female and male body mass and length of head-bill using analyses of variance (PROC GLM).

As data for $CORT_f$ response were only collected on one site and from one nestling per box, I analysed data with analysis of variance (PROC GLM). I considered 5 models to examine the effect of treatment, hatching date and insect biomass on $CORT_f$. Due to small sample size and to reduce the risk of over-parameterization, interactions were not considered. Furthermore, there is some evidence that CORT alone or in conjunction with anti-parasitic treatments, may influence size and growth of body components (Bortolotti et al. 2009*b*). Specifically, high levels of CORT may inhibit size and growth, whereas anti-parasitic treatments may enhance size and growth. Therefore, I considered models that incorporated effects of $CORT_f$ alone and with treatment on nestling size and growth using analysis of variance (PROC GLM).

I used an information-theoretic approach (Akaike's Information Criterion adjusted for small sample size; AIC_c) to examine the relative support for models about variation in nestling quality or $CORT_f$ (Burnham and Anderson 2002). A Kenward-Roger correction (Kenward and Roger 1997) was used to calculate the denominator degrees of freedom for linear mixed models. Within each candidate set, a model with the smallest AIC_c value was considered the most parsimonious, but models within 2 AIC_c units of the best-approximating model ($\Delta AIC_c < 2$) were considered competitive (Burnham and Anderson 2002). The $\beta \pm$ SE of the most parsimonious model are reported unless stated otherwise.

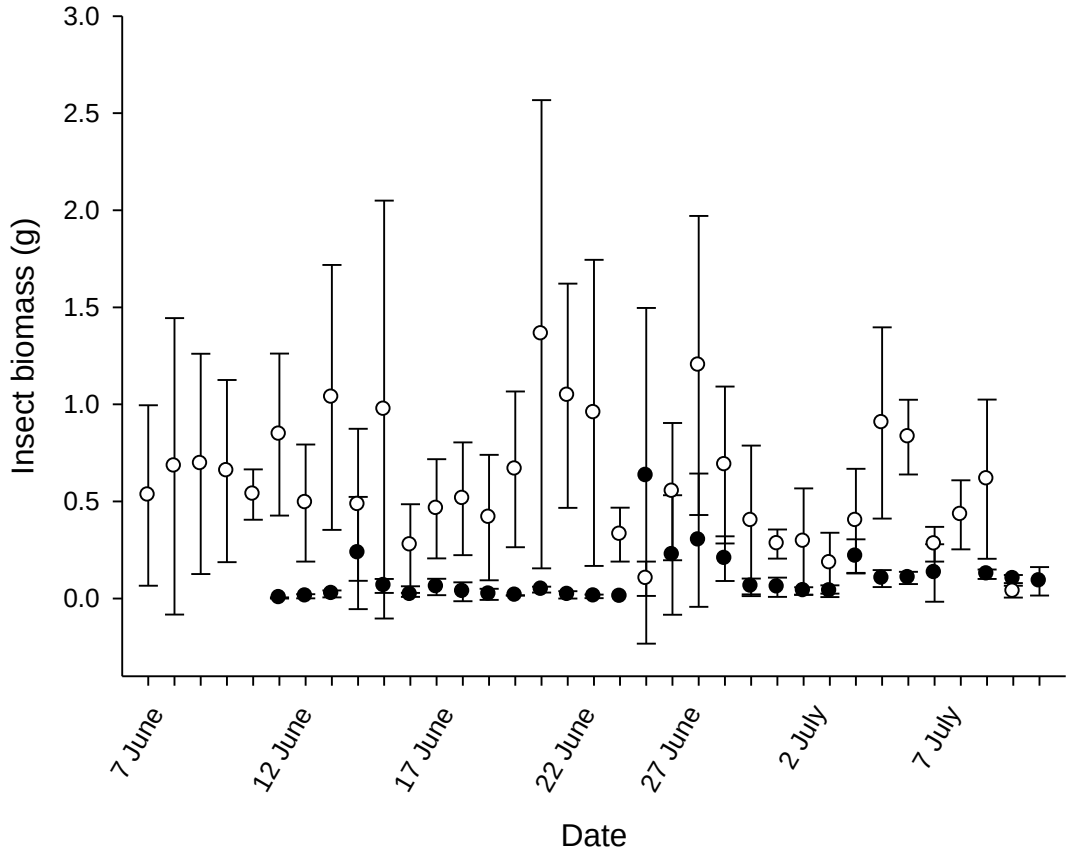


Fig. 2.1. Insect biomass (mean ± SD) corrected for wind speed by sampling date at Prince George, British Columbia (closed circles), and the St. Denis National Research Area, Saskatchewan (open circles), 2007. The covariate used in analyses, mean insect biomass, was calculated per nest and considered insect biomass averaged over the period from when nestlings were aged 2-16 days.

2.3 RESULTS

2.3.1 Parasites

Numbers of blow flies per nestling (n = 75 nests) were best explained by a model that incorporated effects of treatment, clutch initiation date and site (Table 2.1). Permethrin treatment was effective in reducing numbers of blow flies (β = -3.363 ± 0.684; Fig. 2.2). The most parsimonious model for estimated numbers of fleas per nestling (n = 39) included treatment and clutch initiation date (Table 2.1). Permethrin treatment also was effective in reducing numbers of fleas (β = -0.951 ± 0.403). A second well-supported

model suggested an interaction between permethrin treatment and site. Further investigation revealed a strong effect of permethrin on numbers of fleas in nests at PG (β = -2.358 ± 0.917; n = 16) but not at SDNRA (β = -0.529 ± 0.436; n = 23; Fig. 2.2).

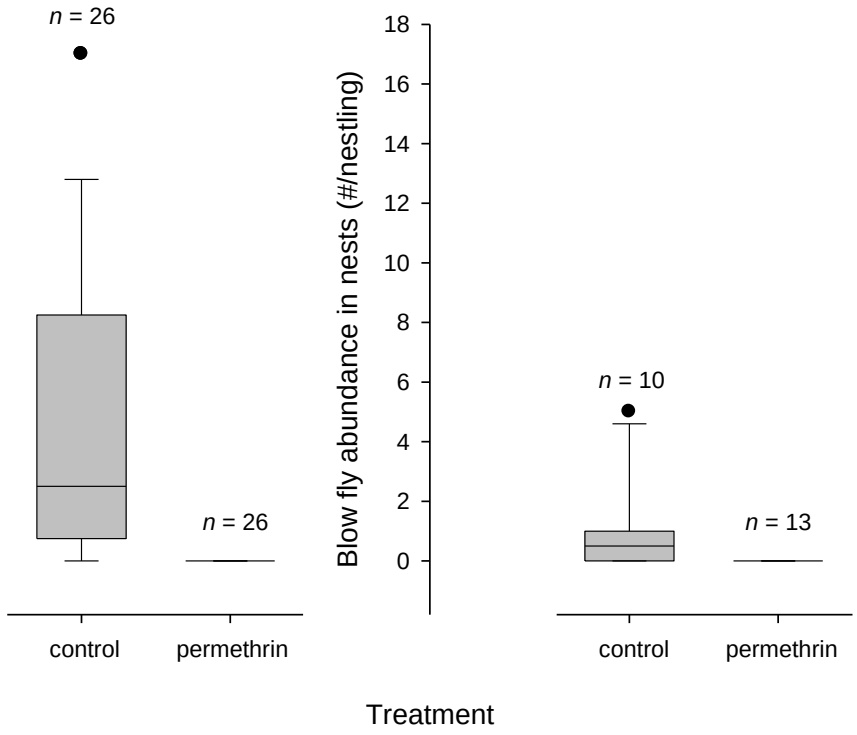
To further investigate the effects of clutch initiation date, site and an interaction between clutch initiation date and site on blow flies and fleas, I considered control nests only (blow flies: n = 36; fleas n = 18). The most parsimonious model suggested that nests contained more blow flies at PG (β = 2.883 ± 1.570; Fig. 2.2) and that, contrary to expectation, the numbers of larval blow flies decreased with later clutch initiation dates (β = -0.457 ± 0.211). Variation in abundance of fleas was best explained by clutch initiation date, but the effect was negligible (β = 0.043 ± 0.101). There was no association between the numbers of blow flies and fleas in control nests (r = 0.007; n = 18).

Table 2.1. Model selection for factors influencing number of fleas and larval blow flies per nestling in nests of tree swallows (*Tachycineta bicolor*) near Prince George, British Columbia, and at the St. Denis National Research Area, Saskatchewan, 2007. Only models with $\Delta AIC_c < 2$ and the intercept only (null) model are presented.

Response variable	**Model structure**[a]	**K**[b]	**-2logL**[c]	**AIC_c**[d]	**ΔAIC_c**[e]	**ω_i**[f]
Number of larval blow flies in nests	Site + Treat + CID	5	375.21	386.08	0.00	0.57
	Null	2	403.97	408.14	22.05	0.00
Estimated number of fleas in nests	Treat + CID	4	213.36	222.54	0.00	0.25
	Treat + Site + Treat*Site	5	210.80	222.62	0.08	0.24
	Treat + CID + Site	5	211.92	223.74	1.20	0.14
	Treat + Site	4	215.14	224.31	1.78	0.10
	Null	2	222.31	226.64	4.11	0.04

[a] Factors included Prince George, British Columbia or St. Denis, Saskatchewan (Site), treatment with permethrin (Treat), clutch initiation date (CID), and an intercept only model (Null). Models with interactions (*) between factors also included the main effects.
[b] Number of estimable parameters.
[c] Deviance.
[d] Akaike's Information Criterion corrected for small sample size.
[e] Difference in AIC_c values between each model and the model with the lowest AIC_c value.
[f] Estimates of the likelihood of the model, given the data; normalized to sum to 1 (Burnham and Anderson 2002).

(a)


n = 26
n = 26
n = 10
n = 13
Blow fly abundance in nests (#/nestling)
0
2
4
6
8
10
12
14
16
18
control
permethrin
control
permethrin
Treatment

(b)

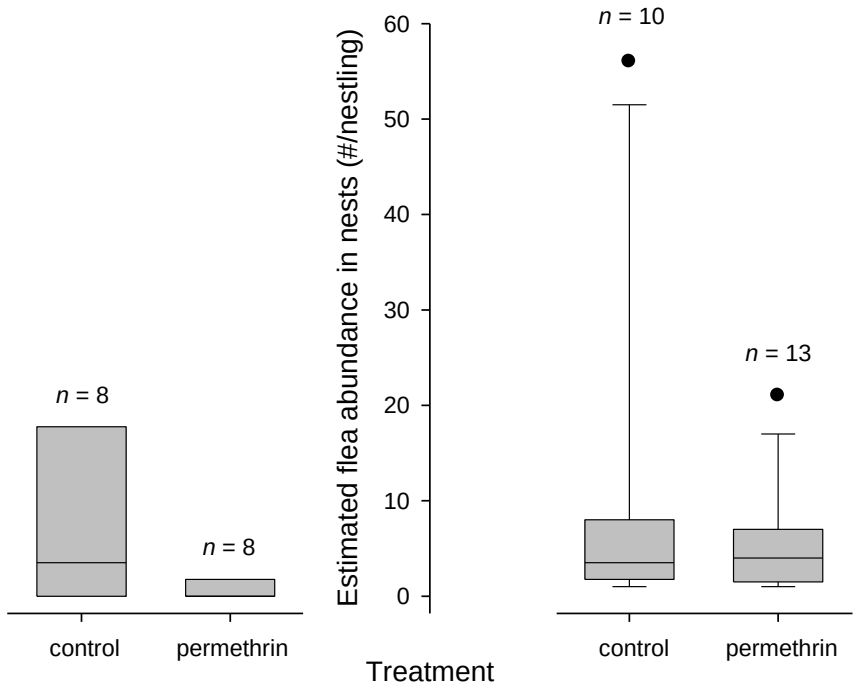

n = 8
n = 8
n = 10
n = 13
Estimated flea abundance in nests (#/nestling)
0
10
20
30
40
50
60
control
permethrin
control
permethrin
Treatment

Fig. 2.2. Blow fly ((a) left = PG and right = SDNRA) and estimated abundance of fleas per nestling ((b) left = PG and right = SDNRA) in nests of tree swallows (*Tachycineta bicolor*) treated with water (control) or an insecticide (permethrin) at Prince George (PG), British Columbia, and the St. Denis National Research Area (SDNRA), Saskatchewan, 2007. The box represents the interquartile range (25-75%), the horizontal line represents the median, the bars extending above and below the box represent maximum and minimum observations, respectively; outliers are represented by circle symbols. Due to small sample size, maximum and minimum observations and outliers could not be computed for abundance of fleas at PG, where estimated abundance of fleas per nestling ranged from 0-36 and 0-4 in control and permethrin treated nests, respectively.

2.3.2 Nestling size and growth

Many of the top models describing nestling size and growth included a treatment by insect biomass interaction. To investigate these interactions, data were analyzed in two ways: (1) the effect of treatment at low (≤ median) and high (> median) levels of insect biomass was considered and (2) the effect of insect biomass was analysed separately for each treatment.

Nestling body mass at day 16 both at PG (n = 266) and SDNRA (n = 125) was best explained by the model including treatment, insect biomass and a treatment by insect biomass interaction (Table 2.2), although none of the factors, including treatment, were informative. Similarly, length of the head-bill of nestlings at day 16 at PG (n = 266) and SDNRA (n = 125) was best described by treatment, insect biomass and a treatment by insect biomass interaction (Table 2.2), although none of the factors, including treatment, was precisely estimated (as judged by SE relative to parameter estimates) at SDNRA. Examination of the interaction at PG indicated that nestlings in treated boxes had longer head-bill lengths at day 16 during periods of high insect biomass (β = 0.414 ± 0.165; n = 111) but not at low levels of insect biomass (β = 0.100 ± 0.145; n = 155; Fig. 2.3). At SDNRA, length of head-bill was also well described by the insect biomass-only model (Table 2.2), but this effect was trivial (β = -3.336 ± 3.063).

The most parsimonious model for length of ninth primary feather at day 16 included treatment, insect biomass and a treatment by insect biomass interaction both at PG (n = 264) and SDNRA (n = 125; Table 2.2). All factors, including treatment, were

imprecisely estimated at SDNRA. Examination of the interaction at PG indicated that nestlings in treated boxes had shorter primary feathers at day 16 as insect biomass increased (β = -98.202 ± 45.810; n = 129) but there was no such relationship for nestlings in control boxes (n = 135; Fig. 2.4).

Variation in growth of body mass was best explained by the insect biomass model at PG (n = 265) and the null model at SDNRA (n = 109; Table 2.2). An increase in insect biomass was associated with slower mass gain at PG but this relationship was not precisely estimated (β = -0.631 ± 0.325). Two models were competitive for describing growth of head-bill at PG (n = 264; Table 2.2), the null and hatching date models. Growth rate of head-bill decreased with hatching date (β = -0.00396 ± 0.00097). Head-bill growth rate was best explained by the null model at SDNRA (n = 112; Table 2.2). Multiple plausible models were selected to explain growth of ninth primary feather at PG (n = 258) and SDNRA (n = 125; Table 2.2) but all factors were uninformative. At PG and SDNRA, models including treatment were not competitive or treatment was poorly estimated, suggesting that treatment was a poor predictor of the rate of nestling growth.

Table 2.2. Model selection for fate, local recruitment, size, growth, T-cell mediated immunity and feather corticosterone levels of nestling tree swallows (*Tachycineta bicolor*) near Prince George, British Columbia (PG), and at the St. Denis National Research Area, Saskatchewan (SDNRA), 2007. Only models with $\Delta AIC_c < 2$ and the intercept only (null) model are presented with the exception of nestling fate at SDNRA where all 7 models considered were statistically plausible but parameters were poorly estimated.

Response variable	**Site**	**Model structure**[a]	**K**[b]	**-2logL**[c]	**AIC_c**[d]	**ΔAIC_c**[e]	**ω_i**[f]
Fate[g]							
	PG	Hatch_date	3	39.33	43.84	0.00	0.70
		Treat + Hatch_date	4	38.81	45.68	1.83	0.28
		Null	2	50.48	52.73	8.89	0.01
Local recruitment[g]	PG	Insect	4	48.14	52.65	0.00	0.52
		Null	2	55.65	57.90	5.25	0.04
	SDNRA	Null	2	31.34	33.89	0.00	0.27
		Treat	3	28.76	33.90	0.01	0.27
		Hatch_date	3	30.46	35.60	1.71	0.11
		Treat + Hatch_date	4	27.76	35.76	1.87	0.11
Mass at 16 d old							
	PG	Treat + Insect + Treat*Insect	6	930.14	942.46	0.00	0.89
		Null	3	949.60	955.69	13.23	0.00
	SDNRA	Treat + Insect + Treat*Insect	6	379.44	392.16	0.00	0.89
		Null	3	395.47	401.67	9.51	0.01

Length of head-bill at 16 d old							
	PG	Treat + Insect + Treat*Insect	6	453.10	465.43	0.00	0.75
		Null	3	466.29	472.38	6.95	0.02
	SDNRA	Treat + Insect + Treat*Insect	6	202.59	215.30	0.00	0.43
		Insect	4	207.09	215.43	0.12	0.40
		Null	3	212.35	218.55	3.25	0.08
Length of ninth primary feathers at 16 d old	PG	Treat + Insect + Treat*Insect	6	1496.48	1508.81	0.00	0.99
		Null	3	1521.55	1527.65	18.84	0.00
	SDNRA	Treat + Insect + Treat*Insect	6	604.79	617.50	0.00	0.96
		Null	3	625.98	632.17	14.68	0.00
Mass growth rate constant							
	PG	Insect	4	-801.97	-793.82	0.00	0.63
		Null	6	-798.69	-792.60	1.22	0.34
	SDNRA	Null	3	-232.74	-226.51	0.00	0.56
		Insect	4	-234.16	-225.78	0.73	0.39
Head-bill growth rate constant							
	PG	Null	3	-1098.22	-1092.13	0.00	0.41

		Hatch_date	4	-1100.22	-1092.06	0.07	0.40
		Insect	4	-1098.60	-1090.44	1.68	0.18
	SDNRA	Null	3	-412.78	-406.56	0.00	0.82
Ninth primary feather growth rate constant	PG	Insect	4	242.13	250.29	0.00	0.54
		Treat + Insect + Treat*Insect	6	239.18	251.51	1.22	0.29
		Null	3	247.43	253.52	3.23	0.11
	SDNRA	Insect	4	51.91	60.24	0.00	0.41
		Treat + Insect + Treat*Insect	6	48.19	60.90	0.66	0.30
		Null	3	55.31	61.51	1.27	0.22
Phytohemagglutinin response							
	PG	Insect	4	-61.30	-52.80	0.00	0.84
	SDNRA	Insect	4	24.52	33.69	0.00	0.37
		Null	3	24.89	34.07	0.37	0.31
		Treat + Insect + Treat*Insect	6	20.13	34.76	1.07	0.22
Feather corticosterone	SDNRA	Treat	3	75.61	82.94	0.00	0.34
		Treat + Hatch_date	4	73.89	84.25	1.31	0.18
		Null	2	79.80	84.43	1.49	0.16

[a] Factors included treatment with permethrin (Treat), mean insect biomass (Insect), hatching date (Hatch_date), and an intercept only model (Null). Models with interactions (*) between factors also included the main effects.
[b] Number of estimable parameters.
[c] Deviance.
[d] Akaike's Information Criterion corrected for small sample size.
[e] Difference in AIC_c values between each model and the model with the lowest AICc value.
[f] Estimates of the likelihood of the model, given the data; normalized to sum to 1 (Burnham and Anderson 2002).
[g] Summarized by nest.

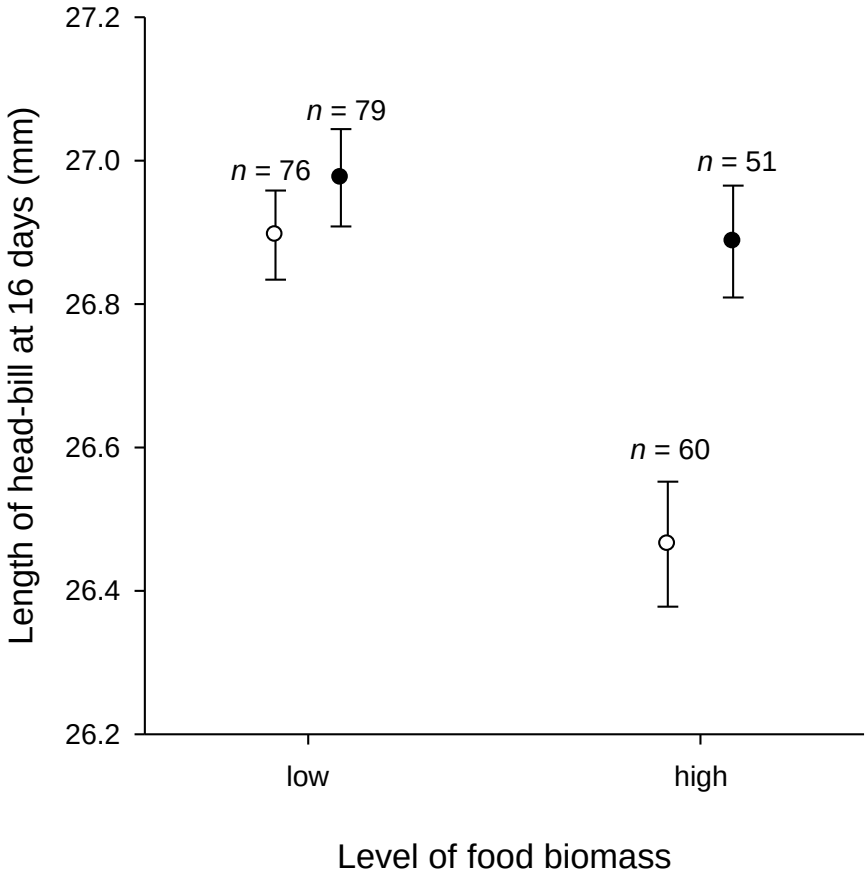


Fig. 2.3. Levels of insect biomass (low ≤ median, high > median) relative to length of head-bill (± SE) of 16 day-old nestling tree swallows (*Tachycineta bicolor*) in nests treated with permethrin (closed circles) and controls (open circles) at Prince George, British Columbia, 2007.

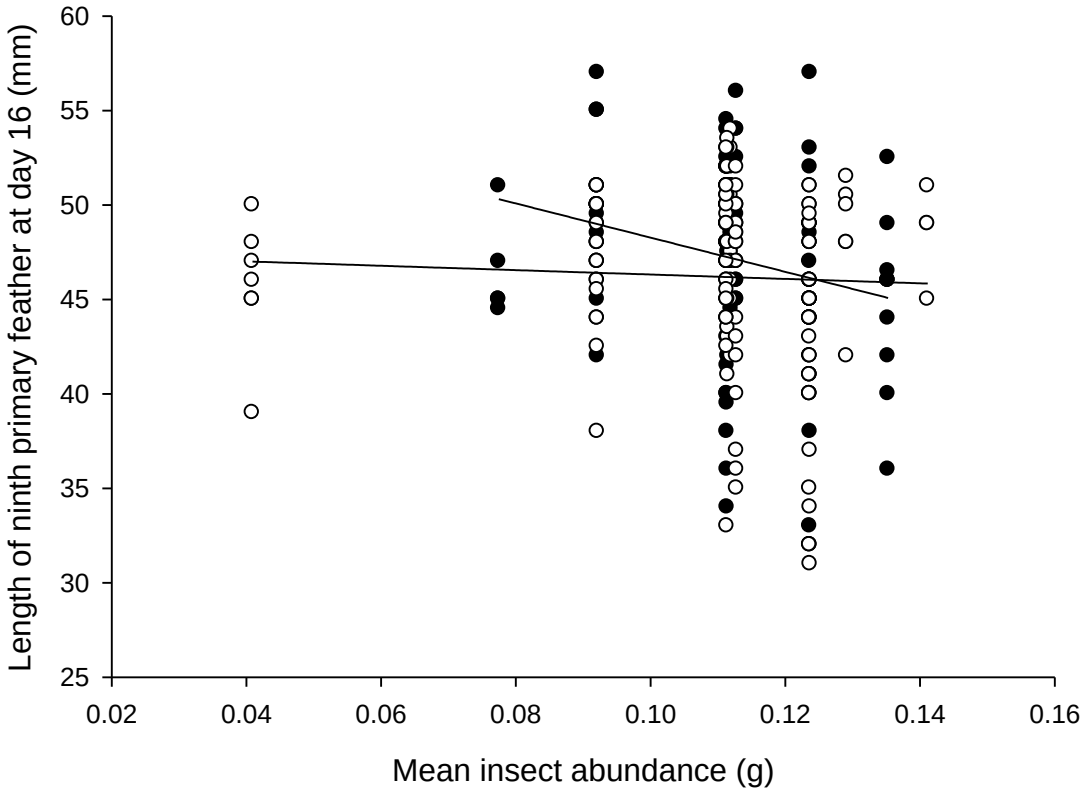


Fig. 2.4. Length (mm) of ninth primary feather at day 16 of nestling tree swallows (*Tachycineta bicolor*) in nests treated with permethrin (closed circles; $n = 129$) and controls (open circles; $n = 135$) relative to mean insect biomass (and associated linear trend lines) at Prince George, British Columbia, 2007.

2.3.3 Nestling survival and recruitment index

Nest success was high at both sites in 2007. One control nest at PG failed during incubation. Two treated nests at PG failed early during the nestling stage; adult trapping likely led to abandonment at one nest and the other failed due to abandonment or adult death. No nests failed at SDNRA. Fourteen nestlings died prior to fledging at PG (1 nestling in 8 nests and 2 and 4 nestlings in 1 nest each). Nine nestlings died prior to fledging at SDNWA (1 nestling in 3 nests and 2 and 4 nestlings in 1 nest each). Nestling fate summarized by nest at PG was best explained by a hatching date model (Table 2.2), with all nestling mortality occurring during the second half of the nesting season ($\beta = 0.288 \pm 0.135$; $n = 51$). All 7 models describing nestling fate at SDNRA ($n = 25$) were

competitive ($\Delta AIC_c < 2$), indicating a high degree of model uncertainty, and no factor was precisely estimated. A total of 17 (PG) and 8 (SDNRA) nestlings recruited locally. Each recruit at SDNRA originated from a different nest whereas 4 nests (3 of which were treated with permethrin) at PG had 2 recruits each. Of the 4 nests containing 2 recruits each, 1 control nest at PG was removed from these and subsequent analyses because it hatched 4 days later than the next latest nest and had no treatment match. Local recruitment of nestlings summarized by nest at PG was best explained by an insect biomass model (Table 2.2), with recruitment at PG (n = 51) being negatively related to insect biomass (β = -0.647 ± 0.288). Nestling recruitment at SDNRA (n = 25) was best explained by two models, null and treatment models (Table 2.2). Although results suggest that nestling return rate was greater in treated nests at SDNRA, the estimate was imprecise (β = 0.728 ± 0.477).

2.3.4 Nestling physiology

Cell-mediated immune response by nestlings at PG (n = 85; Table 2.2) appeared to increase with increasing insect biomass (β = 6.071 ± 2.154), but CMI was unrelated to treatment. The best-supported models pertaining to cell-mediated immune response at SDNRA (n = 46; Table 2.2) suggested that the relationships between CMI and covariates were weak.

I investigated the relationship between $CORT_f$ and treatment, hatching date and mean insect biomass at SDNRA (n = 22; Table 2.2). $CORT_f$ levels were lower for nestlings in treated (mean = 3.671 ± 0.501) versus control (mean = 4.912 ± 0.278) nests (β = -1.242 ± 0.606). Despite hatching date being included in a plausible model (Table 2.2), the relationship between corticosterone levels and hatching date was weak (β = -0.098 ± 0.079). I found no evidence of a relationship between $CORT_f$ and nestling size or growth measurements (all P > 0.25).

2.3.5 Parental quality

I investigated differences in indices of parental quality between sites and seasonal variation of these indices within site. Clutch size was smaller at PG than SDNRA (β = -0.422 ± 0.152; n = 76) but brood size at hatching did not differ between sites. Females (n = 74) at PG were lighter (β = -1.694 ± 0.330) and had shorter head-bills (β = -0.708 ± 0.127) than those at SDNRA; males (n = 75) at PG also were lighter (β = -1.567 ± 0.245) and had shorter head-bills (β = -0.956 ± 0.145). To obtain an index of body condition for adults, I used residuals from linear regressions between body mass and length of head-bill. Both females (β = -0.703 ± 0.311) and males (β = -0.845 ± 0.254) were in poorer condition at PG compared to SDNRA, suggesting the lower body mass of adults at PG was not simply a reflection of their smaller structural size. Of all females breeding at each site, just over one quarter at PG were young birds in their first breeding season, whereas only 1 (< 1%) one-year-old female bred at SDNRA and was not a part of this study. Excluding young females from the data set revealed similar results (β = -0.723 ± 0.337), suggesting that differences in condition of females was not simply an artefact of site-specific differences in age structure of the breeding population. Furthermore, there was no indication that young birds bred significantly later than older birds at PG (β = -0.105 ± 0.101; n = 52). At PG brood size at hatch (n = 51) showed a marginal seasonal decline (β = -0.107 ± 0.057; n =51). No other index of parental quality that I examined varied seasonally at PG or SDNRA.

2.4 DISCUSSION

I tested key predictions of the date hypothesis by determining whether nest parasite abundance increased as the breeding season progressed and subsequently reduced indices of nestling quality and survival. Contrary to expectation, there appeared to be fewer blow flies in nests of late breeders. This trend has been previously documented (Hori and Iwasa 1988, Johnson et al. 1991), albeit less frequently than a seasonal increase (Pinkowski 1977, Wittmann and Beason 1992, Merino and Potti 1995) or no seasonal change in blow fly abundance (Bortolotti 1985, Hurtrez-Boussès et al. 1998, Dawson et al. 2005a, O'Brien and Dawson 2008). Annual patterns in nestling

quality and survival do not always decline seasonally and in some years late-hatched nestlings are either better quality (Christe et al. 2001) or more likely to survive (Harriman et al. unpublished data) than early-hatched nestlings. In my study, trends in the abundances of blow flies (both sites) and biomass of insects (PG only) were indicative of seasonally improving environmental conditions.

Permethrin treatment was effective in reducing parasite numbers in nests. However, in accordance with previous studies ((size: Merino and Potti 1998; Thomas and Shutler 2001; Shutler et al. 2004) (growth: Roby et al. 1992; Wittmann and Beason 1992) (immunity: Saino et al. 1998; Tschirren et al. 2007; Brommer et al. 2011)) there were few detectable effects of parasites on nestling size, growth and immunity. Numbers of blow flies at PG were comparable to those measured in 2003, when a negative effect of parasitism on PHA response was detected (Dawson et al. 2005a, O'Brien and Dawson 2007). Estimates of flea loads were similar to those previously recorded at PG (Dawson 2004) but lower at SDNRA (Shutler et al. 2004). Few detectable effects of parasites on nestling quality may have been a result of pyrethroid toxicity. The International Programme on Chemical Safety of the World Health Organization included some pyrethroids in 1990 Environmental Health Criteria documents and described their toxic effects on birds and mammals as low to very-low. However, a recent study suggests that effects of parasites on nestling quality in cavity-nesting birds may be underestimated as a result of pyrethroid toxicity (López-Arrabé et al. 2014).

Negative effects of parasites may be more pronounced during periods of low food abundance (Johnson and Albrecht 1993, Thomas et al. 2007). Indeed, negative effects of parasites were only apparent when food (i.e., insect) biomass was considered. When food was less abundant (i.e., early in the breeding season), offspring in treated nests at PG had longer primary feathers at day 16 than control nestlings, but the difference in length of primary feathers between these two groups diminished as food supply increased. Nestlings from treated nests raised during periods of high food abundance (i.e., later in the breeding season) had longer head-bills then their control counterparts and developed head-bills of similar length to those of early-hatched nestlings. Brommer et al. (2011) reported differences in length of tarsus and body mass in response to ectoparasite infestation only when nestlings were provided with supplemental food and hypothesized

that parasitized nestlings would allocate supplemented energy to immune function rather than to size or growth. However, like Brommer et al. (2011), I found no relationship between response to PHA by nestlings and parasite treatment or nestling size or growth. Results suggest that early- and late-hatched nestlings at PG allocated energy differently in response to parasites. I found a disproportionate benefit of parasite removal on length of primary feather for early-hatched nestlings, indicating greater energetic constraints early in the breeding season (O'Brien and Dawson 2008). Length of flight feathers is likely an important factor influencing timing of fledging (Saino et al. 1998). Tree swallows nestlings do not attain adult length of primary feather in the nest and early-hatched fledglings may have more time for feather growth prior to migration than late-hatched fledglings (O'Brien and Dawson 2008); therefore, early-hatched nestlings may only allocate energy to flight feather growth when pressures of parasites are alleviated. There was no effect of anti-parasite treatment on nestling body mass, which is an important predictor of first-year survival in tree swallows (Shutler et al. 2006). Given the potential consequences of shorter flight feathers and lower body mass, late-hatched nestlings may have allocated energy to these traits rather than to structural size (i.e., length of head-bill). Skeletal growth of tree swallows is often completed by day 16 (Wiggins 1990), thus this ontogenetic effect of parasitism for late-hatched nestlings may be permanent (Potti and Merino 1996).

Unlike at PG, I did not detect a cost of parasitism on nestling size at SDNRA. Nestlings on these two sites experienced different environmental conditions, with birds at SDNRA having lower blow fly intensities in nests and generally greater food biomass. Nest parasite pressure at SDNRA may have been insufficient to influence nestling growth or size. Shutler et al. (2004) investigated the effects of fleas on nestlings at SDNRA, and despite greater abundances of fleas during that study, no negative effects were detected. Conversely, greater food supply may have alleviated any costs of parasitism via increased feeding frequency to nestlings by parents (Johnson and Albrecht 1993, Christe et al. 1996, Hurtrez-Boussès et al. 1998, but see Thomas and Shutler 2001, Wesolowski 2001, Tripet et al. 2002). Parents at SDNRA may have been more able to increase feeding in response to parasitism, yet Bortolotti et al. (2011) found no difference in feeding rates or seasonal changes in feeding frequency in response to insect biomass at PG or SDNRA in

the year following this study. Potential differences in diet composition of tree swallows at these sites are unknown, and increased selection of profitable prey items by tree swallows has been documented when insect abundance is high (Quinney and Ankney 1985, McCarty and Winkler 1999). Skeletal growth in tree swallows is limited by calcium (Dawson and Bidwell 2005) and O'Brien and Dawson (2008) suggested that regional differences in the availability of dietary calcium may contribute to observed differences in skeletal size or growth in response to parasites in bluebirds. Finally, parents at SDNRA may have been of higher quality, and thus either directly compensated for costs associated with parasitism or produced nestlings that were able to do so. Parents at SDNRA were heavier, structurally larger and females produced larger clutches. Occupancy rates at SDNRA were high, which likely resulted in greater competition for nest boxes and possibly resulted in higher quality individuals securing nest sites. Females rarely breed during their first breeding season (second year females) at SDNRA. No female included in this study at SDNRA was one year old, whereas 27% of females at PG were yearlings.

Contrary to previous work (Bortolotti et al. 2009*b*), $CORT_f$ was lower for nestlings raised in treated boxes than those raised in control boxes at SDNRA. Effects of parasites feeding on nestlings have been attributed to direct loss of nutrients and changes in metabolic capacity (Simon et al. 2004). CORT facilitates energy availability (Romero 2004), and the documented difference in $CORT_f$ may indicate an energetic adjustment in response to parasite removal. Interestingly, no other measurement of nestling quality was affected by treatment at SDNRA. Thus, costs of parasites did not translate into differential size, growth or response to PHA at this site, but more cryptic effects of parasitism were evident in $CORT_f$ levels, indicating a potential energy savings for nestlings raised in boxes with fewer parasites. Variation in CORT, and how it is secreted, during development has been linked to components of fitness, specifically by influencing subsequent incubation behaviour and feeding effort (Spencer et al. 2010), male dominance (Spencer et al. 2005) and recruitment (Blas et al. 2007). My study was not designed to address downstream consequences of nestling CORT secretion. However, my results show that differences in parasite intensity can produce variation in $CORT_f$ in nestlings.

Brood size at hatch and nestling mortality and recruitment decreased seasonally at PG despite an apparent increase in food biomass during the nestling period. Consistent with a central prediction of the parental quality hypothesis, early-nesting parents produced nestlings with similar length of primary feathers to their late-nesting counterparts despite lower levels of food abundance and greater intensities of blow fly infestation. Consistent with predictions of the date hypothesis, early nestlings invested in primary feather growth to attain the longest primary feathers when environmental conditions were improved by removal of parasites. Furthermore, early nesting parents produced nestlings with similar (treated) or longer (control) length of head-bill than late nesting parents and removal of parasites was related to longer length of head-bill in late-hatched nestlings, findings which are consistent with both the quality and date hypotheses. Although my evidence supporting predictions of the parental quality hypothesis is indirect, observing the opposite than predicted trend at PG (i.e., late nestlings disproportionately affected by parasites despite the positive relationship between indices of environmental quality and hatching date) provides support nonetheless. Predictions of the parental quality hypothesis are further supported by seasonal declines in brood size, nestling survival and recruitment (although these were not correlated with parasite loads). Other studies have found support for predictions of both the date and quality hypotheses for some measures of reproductive success, namely clutch size, fledging success and local recruitment (review in Verhulst and Nilsson 2008). To my knowledge, this is the first study to document an interactive effect of date and seasonal variation in parental quality on nestling quality with respect to parasites.

Results from this study demonstrate that both parental and environmental (parasite loads) quality were important predictors of nestling quality at PG but not at SDNRA. With the exception of PHA response, at PG the relationship between food biomass and nestling quality (size, survival) was opposite to predictions of the date hypothesis. Food supply increased seasonally and this strong relationship may indicate that the occurrence of food and hatching date in models are reflections of the same factor: parental quality. Negative effects of nest parasites were documented at PG, where lengths of primary feather and head-bill of nestlings were affected. Interestingly, nestlings at SDNRA likely responded to energy lost to parasites by up-regulating their metabolism as

demonstrated by increased levels of $CORT_f$. I suggest that it was within the capacity of SDNRA nestlings to deal with these parasite loads as there were no other effects of parasites on nestling quality. Ultimately, it appears that parental quality rather than environmental quality during the breeding season had the greatest effect on tree swallow reproductive success at PG as nestling survival and local recruitment declined seasonally regardless of treatment and despite increasing food biomass during the nesting period. These findings are contrary to the preeminent idea that food availability is the most important factor influencing seasonal variation in reproductive success of many avian species. In Chapter 3, I used a robust experimental approach to investigate how food abundance may act as a mechanism of deteriorating environmental conditions.

CHAPTER 3: SEASONAL PATTERNS IN REPRODUCTIVE SUCCESS OF TEMPERATE-BREEDING BIRDS: EXPERIMENTAL TESTS OF ALTERNATE HYPOTHESES

3.1 INTRODUCTION

Organisms living in seasonal environments have a limited time to reproduce and a decline in fitness-related traits with later breeding dates has been documented in diverse plant and animal taxa (Kelly and Levin 2000, Varpe et al. 2007, Anderson et al. 2010, Uller and Olsson 2010). Declines in reproductive success with later nesting dates has been particularly well documented in temperate-breeding birds for which declines in clutch size (Winkler and Allen 1996, Öberg et al. 2013, Winkler et al. 2014) and offspring quality (Gebhardt-Henrich and van Noordwijk 1991, Siikamäki 1998, Dubiec and Cichoń 2001), survival (Shutler et al. 2006, Grüebler and Naef-Daenzer 2008, Gurney et al. 2012, Öberg et al. 2013) and longevity (Saino et al. 2012) have been reported. Decisions about timing of breeding and intensity of reproduction have fitness consequences (Daan and Tinbergen 1997a) which are likely mediated both by individual and environmental quality (Reed et al. 2009), these being the two primary hypotheses proposed to explain seasonal variation in reproductive success.

The quality hypothesis asserts that early-breeding individuals benefit from better phenotypic quality or are in better condition and/or breed on higher quality territories

than late-breeding individuals (Price et al. 1988, Daan et al. 1990, Verhulst and Tinbergen 1991). The date hypothesis predicts that seasonally declining reproductive success is causally related to timing of breeding and is a response to a seasonal deterioration in environmental quality (Perrins 1970, Verhulst and Nilsson 2008). The two hypotheses are not mutually exclusive, and their effects may be manifested simultaneously, at different times throughout the breeding season or at different life-history stages (Verhulst et al. 1995, Grüebler and Naef-Daenzer 2010, Gurney et al. 2012). Aspects of both parental and environmental quality have important consequences for components of fitness in birds. Verhulst and Nilsson (2008) suggest that the value of timing studies is to identify when variables associated with environmental quality influence reproductive success and to identify the mechanism(s) mediating a seasonal deterioration in environmental quality. Knowledge of these relationships is particularly important in making predictions about environmental effects on avian populations under changing climatic conditions (Lyon et al. 2008, Verhulst and Nilsson 2008) and substantiation of purported mechanisms is essential.

Mechanisms underlying a seasonal decline in environmental quality may be complex; however, food availability is often proposed as the most important factor influencing seasonal variation in reproductive success of many avian species (Perrins 1970, Siikamäki 1998, Verboven et al. 2001). Indeed, since the seminal studies by Lack (1954) and Perrins (1970), it has generally been believed that birds time breeding so the nestling period corresponds with periods of peak food availability for nestlings. The relationship between clutch initiation date and reproductive success has been frequently correlated with seasonal declines in food abundance (Norris 1993; Dawson 2008; Öberg et al. 2013). Furthermore, experimental manipulations of food abundance have demonstrated consequences of seasonally declining food resources on reproductive success (Verboven et al. 2001, Burger et al. 2012). Despite the preeminent idea that seasonally declining food availability is an important factor mediating seasonal trends in fitness in avian ecology, I am aware of only one published experimental investigation about how food abundance may act as a mechanism of deteriorating environmental conditions associated with reduced reproductive success while controlling for parental quality (Siikamäki 1998). This is likely due to the challenge of performing a

manipulation that forces parents to raise their offspring during an unintended period of time (i.e., with different food supplies) without altering parental quality (Verhulst and Nilsson 2008).

I conducted a series of manipulations to test predictions associated with the date hypothesis, while accounting for parental quality, in the tree swallow (*Tachycineta bicolor*) over two breeding seasons and in two distinct locations within their breeding range in Canada. Apparent recruitment rates of tree swallows are negatively related to hatching date (Shutler et al. 2006) and robust tests of this hypothesis are absent among North American aerial insectivores, a guild of birds experiencing population declines in many regions of this continent (Nebel et al. 2010, Shutler et al. 2012). To account for potential effects of parental quality, I paired nests by clutch initiation date and delayed the hatching of one nest within the pair. Subsequently, brood size manipulations were conducted to mimic changes in per capita food abundance (Shutler et al. 2006, Bortolotti et al. 2011). I then examined the effects of manipulations, as well as indices of environmental (e.g., insect biomass) and parental (e.g., parental condition) quality, on nestling quality, fledging success and return rates. If seasonally declining reproductive success was partly attributed to seasonally declining food abundance, I predicted that (i) nestlings in enlarged broods (i.e., with reduced per capita food) would be of lower quality and less likely to survive to fledging or return in subsequent years than their control counterparts and (ii) this relationship would be more pronounced later in the season regardless of when parents initiated nests.

3.2 MATERIALS AND METHODS

3.2.1 Study areas

Research was conducted on tree swallows breeding in nest boxes over two seasons (2008-09) at two widely separated locations. The Saskatchewan site was located on the St. Denis National Research Area (SDNRA; 52^{o}N, 106^{o}W), 40 km east of the city of Saskatoon. This site had few trees and was within an agricultural landscape composed of alfalfa (*Medicago sativa* L.) and brome grass (*Bromus inermis* Leyss) cover, agricultural crops and abundant wetland basins. Nest boxes on SDNRA were attached 1.5

m above ground to metal posts with the box entrance facing southeast. There were 165 boxes in 2008 and 160 in 2009 in the core colony. Nest boxes were arranged in two ways: first, as a continuous series of 115 boxes (placed ~30 m apart) and, second, additional boxes formed 9 (2009) or 10 (2008) distinct "neighbourhoods" of 5 boxes each (30 m spacing). Box occupancy was > 99% in both years.

Data were also collected on two sites, one in each year, in the vicinity of Prince George (53^{o}N, 122^{o}W), British Columbia. These sites (both referred to as 'PG') were within an open agricultural habitat interspersed with small stands of deciduous and coniferous trees. Nest boxes were ~30 m apart and mounted on wooden fence posts. Sites were composed of a series of 123 (2008) and 139 (2009) nest boxes. Box occupancy rates during this study were 61% (2008) and 49% (2009).

3.2.2 Nest monitoring and delay and brood size manipulations

Nest boxes were visited daily to determine clutch initiation and completion dates. When two females began laying within 2 days of each other, each was randomly assigned to either the non-delay (i.e., control) or delay group. On the morning the third egg was laid, all eggs were either picked up and replaced (non-delay) or collected and replaced with solid plastic eggs painted white (delay). Each subsequent egg in the laying sequence was handled (non-delay) or collected and replaced with a dummy egg (delay) the morning that eggs were laid. Collected eggs were transported to the lab and refrigerated at 8^{o}C (Wiggins et al. 1994, Siikamäki 1998). Clutch completion was determined when the clutch size remained the same for 3 days, at which time visits ceased, with the exception of delay nests. To mimic natural hatching asynchrony in delay nests, the first 4 eggs laid were returned 3 days following clutch completion and the remaining 2-4 eggs were returned the next day. Two days prior to the estimated hatching date all nests were visited daily to determine the date of first nestling emergence, hatching success and brood size.

Three nests belonging to the delay group that hatched on the same day and had clutch initiation dates within 2 days of each other were randomly assigned to either brood enlargement, control or reduction manipulation groups. Likewise, three nests belonging

to the non-delay group that hatched on the same day and had clutch initiation dates within 2 days of each other were randomly assigned to either brood enlargement, control or reduction manipulation groups. When nestlings were 2-days-old, they were weighed and 2 nestlings of intermediate mass (i.e., not the smallest or largest) were individually marked with non-toxic marker and removed from reduction nests and placed in enlargement nests. Nestlings in control nests were weighed and returned to their own nest. This resulted in 6 manipulation combinations with nearly equal initial sample sizes of nests: non-delay-enlargement, non-delay-control, non-delay-reduction, delay-enlargement, delay-control, delay-reduction. Nestlings from a single reduced brood were added to enlarged broods with the exception of SDNRA in 2008 when embryo mortality occurred in some delay clutches (see also Wiggins et al. 1998) and resulted in composite broods of nestlings from up to four nests to achieve intended brood sizes.

3.2.3 Adult and nestling measurements

When all viable eggs had hatched, parents were captured at the box and mass (nearest 0.5 g measured with a 60 g spring scale) and length of head-bill (nearest 0.01 mm with dial [SDNRA] or digital [PG] calipers) were recorded. Nestling age was calculated by denoting the presence of the first nestling as day 0 such that all nestlings in a box were assigned the same age. Individual nestlings were uniquely marked with non-toxic markers beginning on day 4 (or day 2 for swapped nestlings) and banded with aluminum bands at 12 (SDNRA) or 16 (PG) days of age. Measurements of mass (nearest 0.25 g measured with a 30 g spring scale) and length of the head-bill (2008 only; as above for adults) were recorded for each nestling every other day from 4- to 16-days-old. In 2009, length of head-bill was measured when nestlings were 16-days-old. Additionally, the length of the ninth primary feather was measured (nearest 0.5 mm with a ruler) every other day when nestlings were 8- to 16-days-old.

In 2008, T-cell-mediated immune function was assessed for two nestlings per box using an injection of phytohemagglutinin (PHA). Two nestlings of intermediate mass within a nest were selected. On day 9, 30 μl of 2 mg/ml of PHA in phosphate-buffered saline was injected into the right wing web and wing web thickness (nearest 0.01 mm)

was measured with a thickness gauge (nearest 0.005 mm at SDNRA, nearest 0.01 mm at PG) just prior to and 24 hour post-injection (Smits et al. 1999). The left wing web was measured to account for growth in web thickness over the 24 hour period. Cell-mediated immune response (CMI) was calculated by determining the difference in web thickness before and after injection and adjusting for growth (O'Brien and Dawson 2008).

All measurements were performed by two observers at PG (one in each year) and two observers at SDNRA with the exception of PHA which was performed by only one observer at SDNRA.

3.2.4 Weather data and insect abundance

Ambient temperature (°C), rainfall (mm) and wind speed (m/s) were recorded on each site annually, with the exception of 18-27 June 2009 at PG when data were collected from a nearby site (10.8 km away) due to an on-site equipment malfunction. Anemometers were located 2 m (SDNRA) and 3 m (PG) above ground. A daily weather index was calculated by summing standardized values (for both sites and years combined) of mean temperature, minimum temperature, total rainfall, mean wind speed and maximum wind speed (Pelayo and Clark 2003). Negative values indicated cool, wet and windy weather conditions.

Passive insect samplers (see Quinney and Ankney 1985 for design) were placed in the vicinity of nest boxes with the opening of the net 2 m above ground (n = 2 and 4 at SDNRA in 2008 and 2009, respectively; n = 2/year at PG). Insects accumulated in jars containing 70% ethanol and were collected and replaced after ~12 (SDNRA) or ~ 24 hours (PG) of sampling. Insects were stored in fresh ethanol until they could be dried and weighed (nearest 0.00001 g with an analytical balance; Harriman et al. 2014). Daily insect biomass was averaged among passive samplers on each site and corrected for sampling duration and mean wind speed during the sampling period (Quinney et al. 1986). Mean weather index and mean insect biomass were calculated for each nest during the period when nestlings were 2- to 16-days-old (i.e., for the duration of nestling measurements plus 2 days prior to the first nestling measurement).

3.2.5 Statistical analyses

Clutch initiations occurred over a narrow range of days at both sites in both years. At SDNRA, > 95% (i.e., principle nesting period) of all clutches in the colony were initiated over a span of 13 days in 2008 and over 11 days in 2009. In 2008, 66 nests were included and spanned the full 13 days of the principal nesting period, whereas, in 2009, 96 nests spanned the entire principal nesting period and also included 3 nests that were initiated relatively late. At PG, > 95% of clutches were initiated within an 11 day period in 2008 and within a 15 day period in 2009. My experiment included 27 and 34 nests and spanned 8 and 10 days of the principal nesting period in 2008 and 2009, respectively. The delay manipulation resulted in a hatching delay of ~5 days (control: mean incubation duration = 13.23 days, SD = 0.70, n = 111; delay: mean incubation duration = 18.50 days, SD = 0.88, n = 112). A 5-day hatching delay represented 38% and 45% (SDNRA) and 45% and 33% (PG) of the principal nesting periods in 2008 and 2009, respectively. Long-term data from the SDNRA suggest that a 5-day delay in breeding could result in a 13% decline in local recruitment of nestlings (Shutler et al. 2006).

Generalized linear models (PROC GLM; SAS Institute Inc., Cary, North Carolina, USA) were used to examine potential differences in clutch size, brood size and adult condition at hatch among treatment groups and between sites and years. I was particularly interested in potential effects of the delay treatment on adult condition, as delayed females experienced extended incubation duration. Pearson correlations (PROC CORR) revealed that body mass of female (n = 221) and male (n = 215) adults at capture were positively correlated with head-bill length (r = 0.462 and 0.346 respectively, Ps < 0.0001) and negatively correlated with age of nestlings (r = -0.394 and -0.198, P < 0.0001 and P = 0.004 respectively). Residuals of adult mass regressed against their head-bill length and age of nestlings at capture were used as an index of adult body condition (O'Brien and Dawson 2013). Eleven models were considered for each sex separately, including interactions among year, site, delay and brood size manipulations.

To investigate potential effects of brood size manipulations on nestling growth, growth rate constants were calculated for each nestling. I used a non-linear procedure to fit logistic models (PROC NLIN) for gain of body mass and growth of head-bill using the Levenberg-Marquardt estimation method. For growth of ninth primary feather, I fit a

linear model (Dawson et al. 2005b). Individuals without complete growth data (days 4 to 16 for mass and head-bill, and days 8 to 16 for primary feather) were excluded. Residuals of nestling mass regressed against length of head-bill at 16-days-old were used as an index of nestling body condition at fledging (PROC GLM; $\beta = 0.941 \pm 0.058$, $n = 1277$).

Although brood size manipulations provided a strong test of varying food abundance (i.e., per nestling) as a mechanism underlying a seasonal deterioration of the environment, other environmental factors could also influence nestling quality. Specifically, climatic variation can alter the quality of nestling tree swallows (McCarty and Winkler 1999, Dawson et al. 2005b) independent of hatching date and parental quality (Dawson 2008), so I considered the effect of the weather index on nestling quality. Delay manipulations were intended to control for parental quality, i.e., individuals that initiated breeding at the same time were assumed to be of similar quality (Ardia 2005a, O'Brien and Dawson 2013). However, parental quality may also be an important predictor of nestling quality, independent of breeding time (Cichoń et al. 2006) and so the index of parental body condition was considered in analyses. Although brood size manipulations alter food available on a per capita basis (Shutler et al. 2006, Bortolotti et al. 2011), I was not able to directly manipulate the food intake of nestlings. Thus, I also included aerial insect biomass in analyses. Finally, brood size manipulations aimed to either increase or decrease intended brood sizes by 2 nestlings. Primarily due to reduced egg hatchability in delayed nests, but also due to other potential patterns in egg hatchability (e.g., annual, seasonal), the difference between intended and actual brood size was considered as an alternative to the categorical variable, brood size manipulation.

Linear mixed models (PROC MIXED) were used to examine the influence of treatments (delay, brood size manipulation), difference between actual brood size and intended brood size (brood size post-manipulation – clutch size), clutch initiation date (standardized to the first clutch initiation date each year at each site), insect biomass, weather index, condition index of female parents of the box nestlings were raised in, site and year (fixed effects) on nestling mass, lengths of the head-bill and primary feather at day 16, growth rates of mass, head-bill and primary feather, body condition and PHA response. These analyses accounted for clustering of data within nest boxes by using nest identity of the box nestlings were hatched in and raised in as random factors.

Predicted relationships between covariates and nestling quality relative to each hypothesis are shown in Table 3.1. Brood size manipulation was correlated with difference in actual from intended brood size, and clutch initiation day was correlated with insect biomass and weather index; therefore these covariates were not included simultaneously in the same model. Year was not included in models for growth of head-bill and PHA response as those data were only collected in 2008. Effects of time of day and nestling mass at injection (fixed effects) on PHA response also were considered (Forsman et al. 2010). The inclusion of identity of hatching and rearing nests as random effects was redundant with respect to cell-mediated immunity of nestlings, likely due to the small sample size. The nest where nestlings hatched ($\beta = 0.017 \pm 0.012$) explained a greater amount of variation in PHA response than nest of rearing ($\beta = 0.011 \pm 0.011$) and was thus included as the single random effect in analyses to account for the potential lack of independence between nestlings raised in the same nest (Barr et al. 2013). I considered 28 *a-priori* models for each response variable (25 for growth of head-bill), including interactions between treatments and treatments and clutch initiation day, and an intercept-only (null) model. Parameters were estimated (β) using restricted maximum likelihood estimation (REML, PROC MIXED). A Kenward-Roger correction (Kenward and Roger 1997) was used to calculate the denominator degrees of freedom for linear mixed models.

The body condition of males raising nestlings was considered in initial analyses and never appeared in models with strong support ($\Delta AIC_c > 7$ for mass at day 16, all others $\Delta AIC_c > 32$, see below for definition of ΔAIC_c; Anderson 2008). No male was captured at 7 nests and to maximize sample size and maintain matched pairs of nests, male body condition was removed from final analyses.

Due to the small numbers of nestlings that either died prior to fledging or recruited locally, I examined nestling fate and local recruitment as binary responses, i.e., considered by nest rather than by individual. Thus, for each nest, all nestlings either fledged or at least one nestling died (fate), and either at least one nestling returned to the breeding population as an adult or none returned (recruitment index). I considered recaptures of marked nestlings until 2012, i.e., 3-4 years following experiments, which was sufficient duration to detect >90% of all recruited offspring at both sites (n = 530 (NWA, 1991-2012) and 137 (PG, 2002-2012) total recruits; VBH, unpubl. data). Logistic

regressions (PROC LOGISTIC) were used to consider the effect of treatments, difference in actual from intended brood size, clutch initiation date, insect biomass, weather index, condition index of female parents of the box nestlings were raised in, site and year on survival to fledging and subsequent local recruitment of nestlings that fledged. I considered 29 *a-priori* models for both response variables, including interactions between delay and brood size manipulations, manipulations and clutch initiation day, and an intercept-only (null) model. The local recruitment index measures return rates and this index should not be considered a surrogate for survival estimates.

I used an information-theoretic approach (Akaike's Information Criterion adjusted for small sample size; AIC_c) to examine the relative support for models about variation in nestling quality (Burnham and Anderson 2002). Within each candidate set, a model with the smallest AIC_c value was considered the most parsimonious, but models within 2 AIC_c units of the best-approximating model ($\Delta AIC_c < 2$) were considered competitive (Burnham and Anderson 2002). The estimates of the likelihood of the model relative to all models considered (Akaike weight; ω_i) were also used make inferences. The $\beta \pm$ SE of the most parsimonious model are reported unless stated otherwise.

Table 3.1. Predicted effect or direction of relationships between covariates and indices of quality of nestling tree swallows for the quality and date hypotheses. A minus (-) symbol indicates a negative effect or direction, plus (+) signifies a positive effect or direction, (o) indicates no effect, and open boxes indicate that the covariate is not applicable to the hypothesis.

Covariate	**Quality**	**Date**
Delay manipulation (delayed vs. non-delayed)	o	-
Brood size enlargement		-
Brood size control		o
Brood size reduction		+
Difference in actual brood size from intended brood size		-
Insect biomass		+
Weather index		+
Clutch initiation date	-	-
Female body condition index	+	

3.3 RESULTS

Clutch size was best explained by a model that included year, site and brood size manipulation (ω_i = 0.34). Clutch sizes were larger in 2008 (β = 0.246 ± 0.099; n = 223) and at SDNRA (β = 0.243 ± 0.110). There was some evidence that clutch sizes of parents raising reduced broods were larger than their control counterparts (β = 0.231 ± 0.117) but there was no difference (β = 0.170 ± 0.118) in clutch size between parents raising control and enlarged broods. This resulted in a smaller difference between brood sizes in reduced and control nests than enlarged and control nests (reduced: mean = 4.16, SD = 0.90, n = 69; control: mean = 5.93, SD = 1.22, n = 86 enlarged: mean = 8.30, SD = 0.86, n = 66) after brood size manipulations. A second well-supported model (ω_i = 0.31) included year and site and corroborated results with respect to these factors.

Brood size at hatch was best explained by the model including year, site, delay treatment and an interaction between year and delay. To investigate these relationships, data were separated by year. In 2008 (n = 93), brood size at hatch was smaller in delayed than non-delayed nests (β = -1.343 ± 0.261) and was smaller at PG than SDNRA, although this site effect was weak (β = -0.429 ± 0.287). In 2009 (n = 130), brood size at hatch was smaller in delayed than non-delayed nests (β = -0.646 ± 0.190) and smaller at PG than SDNRA (β = -1.067 ± 0.215). These results indicate that in both years delay treatment resulted in reduced egg hatchability. There was an attempt to mitigate reduced egg hatchability on brood size at SDNRA in 2008 (see methods above). To determine whether brood sizes post-manipulation differed by year, site and/or delay treatment, 7 models were considered and each included the class variable brood size manipulation (enlarge, control, reduce) to account for different sample sizes between these groups (n = 223). The top model (ω_i = 0.99) included year, site and delay treatment. Brood sizes were larger in 2008 (β = 0.451 ± 0.126), at SDNRA (β = 0.817 ± 0.139) and in non-delayed nests (β = 0.453 ± 0.124) independent of brood size manipulation.

The best-approximating model with respect to female body condition indicated that females at PG were in poorer body condition than those at SDNRA (β = -0.738 ± 0.180; n = 221). Male body condition also was poorer at PG (β = -1.148 ± 0.172; n = 215), and although the top model included year, this effect was negligible (β = -0.282 ±

0.152). There was no indication of an effect of delay treatment on female or male body condition. Furthermore, I investigated whether mean mass of nestlings at day 4 was different between delayed and non-delayed nests in brood size control nests only (PROC GLM). The top-ranked model indicated that mean nestling mass at day 4 was lower at PG than SDNRA ($\beta = -1.133 \pm 0.386$; n = 79) but did not differ by delay treatment ($\beta = -0.243 \pm 0.327$).

3.3.1 Nestling size and growth

Three models were competitive for describing body mass of 16 day-old nestlings ($n = 1277$; Table 3.2). The top-ranked model suggested that nestling mass increased with increasing insect biomass ($\beta = 2.803 \pm 0.496$) and that nestlings in enlarged broods were lighter than those in control broods ($\beta = -0.399 \pm 0.163$) but there was no difference in mass between nestlings in reduced and control broods ($\beta = 0.148 \pm 0.177$). The second best model suggested an interaction between insect biomass and brood size manipulation. To investigate this interaction, data were treated in two ways. First, the effect of insect biomass on nestling mass was considered separately for each brood manipulation category and, second, the effect of the brood size manipulation was considered for nestlings raised during periods of low (≤ median) and high (> median) levels of insect biomass. Nestling mass was positively related to insect biomass at all levels of brood size manipulations. Nestlings in enlarged broods were lighter than those in control broods ($\beta = -0.552 \pm 0.276$, $n = 603$) at low levels of insect abundance, but not at high levels of insect abundance ($\beta = -0.275 \pm 0.206$; $n = 674$; Fig. 3.1). Mass of nestlings in control and reduced broods did not differ at either level of insect biomass. Finally, the third-ranked model indicated that nestlings in enlarged broods were lighter than their control counterparts ($\beta = -0.389 \pm 0.158$), that delayed nestlings were lighter than those in non-delayed nests ($\beta = -0.529 \pm 0.141$) and that females in better body condition raised heavier nestlings ($\beta = 0.286 \pm 0.056$).

Length of primary feathers of 16 day-old nestlings was best described by two models ($n = 1300$; Table 3.2). Both models indicated that nestling primary feathers were longer when mean insect biomass was greater (model 1: $\beta = 10.392 \pm 1.841$, model 2: $\beta =$

10.127 ± 1.837). The top-ranked model also included brood size manipulation, but neither nestlings in enlarged (β = 0.010 ± 0.621) nor reduced (β = 0.933 ± 0.654) broods differed from those in control broods. Length of the head-bill of 16 day-old nestlings (n = 1299) was best described by the model including insect biomass (Table 3.2) and suggested that head-bill of nestlings was longer when nestlings developed during periods of greater insect biomass (β = 2.342 ± 0.228).

Variation in growth of nestling body mass (n = 1273) was best explained by the null model, which indicates that most of the variation in gain of mass can be attributed to random effects of the nest where nestlings were hatched (β = 0.556 ± 0.149) or raised (β = 0.534 ± 0.155). *Post hoc* analyses which considered some variables included in the weather index independently (mean temperature and total rainfall) revealed support for a rainfall model and suggested that greater amounts of total rainfall during the nestling period (days 2 to 16) negatively influenced gain of body mass (β = -0.021 ± 0.007; Table 3.2). Growth rate of head-bill (n = 547) was best explained by the null model, but models incorporating effects of insect biomass (ΔAIC_c = 4.77) and delay treatment (ΔAIC_c = 6.65) had weak support (Anderson 2008). Length of head-bill grew faster with increasing insect biomass (β = 0.029 ± 0.015) and nestlings in delay nests had slower rates of head-bill growth than their non-delayed counterparts (β = -0.011 ± 0.005). The growth of ninth primary feathers (n = 1289) was best explained by an insect biomass model, with faster feather growth at higher levels of insect biomass (β = 0.640 ± 0.147; Table 3.2).

Nestling body condition (n = 1275) was best explained by a model including delay treatment, brood size manipulation and female body condition (Table 3.2). Nestlings in delayed nests were in poorer condition that their non-delayed counterparts (β = -0.323 ± 0.132) as were nestlings in enlarged broods relative to control (β = -0.360 ± 0.149) and reduced (β = -0.479 ± 0.146) broods, with no difference between nestlings in control and reduced broods (β = 0.119 ± 0.161). Females in better body condition raised nestlings with better condition (β = 0.283 ± 0.053).

Cell-mediated immune response by nestlings (n = 168) was best explained by the null model. However, a female condition model had some support (ΔAIC_c = 3.66) and

suggested that CMI response was greater for nestlings raised by females in better condition ($\beta = 0.042 \pm 0.020$).

Table 3.2. Model selection results for analyses that related fate, local recruitment, size, growth, body condition and T-cell mediated immunity of nestling tree swallows (*Tachycineta bicolor*) to measurements of parental and environmental quality. Work was conducted at the St. Denis National Research Area, Saskatchewan, and near Prince George, British Columbia, 2008-09. Only models with $\Delta AIC_c < 4$ and the intercept-only (null) model are presented with the exception of specific models of interest with precise parameter estimates.

Response variable	**Model structure**[a]	**K**[b]	**-2logL**[c]	**AIC_c**[d]	**ΔAIC_c**[e]	**ω_i**[f]
Mass at 16 d old	BroodManip + Insect	7	4525.52	4539.61	0.00	0.27
	BroodManip * Insect	9	4521.63	4539.77	0.16	0.25
	BroodManip + Delay + FCond	8	4523.96	4540.07	0.46	0.21
	FCond + BroodManip * Delay	10	4521.19	4541.36	1.75	0.11
	Global (BroodManip + Delay + FCond + CID + Year)	10	4521.49	4541.67	2.05	0.10
	Null	4	4563.27	4571.30	31.69	0.00
Length of head-bill at 16 d old	Insect	5	2367.73	2377.78	0.00	0.97
	Null	4	2455.12	2463.15	85.37	0.00
Length of ninth primary feathers at 16 d old	BroodManip + Insect	7	7430.88	7444.97	0.00	0.45
	Insect	5	7435.24	7445.29	0.32	0.38
	Insect * CID	7	7433.08	7447.17	2.20	0.15
	Null	4	7467.19	7475.22	30.25	0.00
Mass growth rate constant	Null	4	-3131.22	-3123.19	0.00	0.59
	Rain	5	-3132.38	-3122.33	0.86	0.38
Head-bill growth rate constant	Null	4	-2267.44	-2259.36	0.00	0.88
	Insect	5	-2264.71	-2254.59	4.77	0.08
	Delay	5	-2262.82	-2252.71	6.65	0.03

Ninth primary feather growth rate constant	Insect	5	673.83	683.87	0.00	0.98
	Null	4	690.01	698.04	14.17	0.00
Nestling body condition	BroodManip + Delay + FCond	8	4250.05	4266.16	0.00	0.47
	BroodManip*Delay + FCond	10	4247.31	4267.49	1.33	0.24
	BroodManip + FCond	7	4253.73	4267.82	1.66	0.21
	Null	4	4284.37	4292.40	26.24	0.00
Phytohemagglutinin response	Null	3	83.22	89.37	0.00	0.64
	FCond	4	84.78	93.03	3.66	0.10
Fate[g]	Site	2	176.27	180.33	0.00	0.47
	BroodManip + Insect	4	173.89	182.08	1.75	0.20
	Site + Year	3	176.17	182.28	1.95	0.18
	Insect	2	179.12	183.18	2.85	0.11
	Null	1	209.022	211.04	30.71	0.00
Local recruitment[g]	Delay * CID	4	179.91	188.09	0.00	0.40
	Delay + DiffIntend	3	183.34	189.45	1.36	0.20
	Delay + CID + DiffIntend	4	183.34	191.53	3.43	0.07
	Delay + Year	3	185.67	191.78	3.68	0.06
	Null	1	196.44	198.46	9.01	0.00

[a] Factors included delay treatment (Delay), brood size manipulation (BroodManip), difference between actual and intended brood size (DiffIntend), mean insect biomass (Insect), clutch initiation day (CID), female body condition (FCond), Site, Year, total rainfall (Rain) and an intercept-only model (Null). Models with interactions (*) between factors also included the main effects.
[b] Number of estimable parameters.
[c] Deviance.
[d] Akaike's Information Criterion corrected for small sample size.

[e] Difference in AIC_c values between each model and the model with the lowest AICc value.
[f] Estimates of the likelihood of the model, given the data; normalized to sum to 1 (Burnham and Anderson 2002).
[g] Summarized by nest.

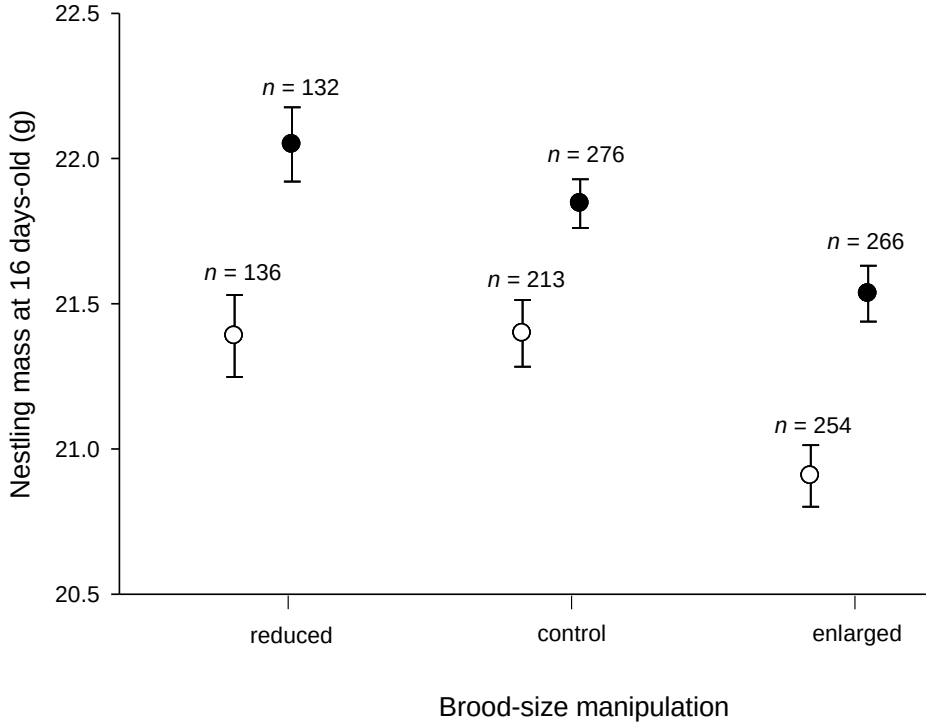


Fig. 3.1. Mean (± SE) mass (g) of 16 day-old nestlings raised during periods of low (open circles) and high (closed circles) levels of aerial insect biomass by brood-size manipulation at the St. Denis National Research Area, Saskatchewan, and Prince George, British Columbia, 2008-09. Number (n) of nestlings shown for each value.

3.3.2 Indices of nestling fate and recruitment

More nestlings died prior to fledging at PG than SDNRA (β = -1.060 ± 0.192; n = 221 nests). A second plausible model suggested that nestling survival was positively associated with insect biomass (β = 6.750 ± 1.302) and that the likelihood of at least one nestling dying prior to fledging was greater in enlarged than control nests (β = -0.612 ± 0.269).

Of 221 nests included in analyses, one nestling recruited from 30 nests, two nestlings returned from five nests (all at SDNRA) and three from one nest (at PG). All nests for which more than one nestling recruited were non-delayed nests and brood sizes had either been reduced or enlarged (i.e., no controls). Multiple recruits were produced from nests spanning a wide range of clutch initiation days (day 3-10). Local recruitment

index was best explained by two models. The top-ranked model revealed an interaction between delay treatment and clutch initiation date. To examine this interaction data were considered in two ways, first by delay treatment and then by early (< median) and late (≥ median) clutch initiation dates. Recruitment index for nestlings in non-delayed nests tended to decline seasonally (β = -0.187 ± 0.106; n = 110) but increased seasonally for nestlings in delayed nests (β = 0.247 ± 0.102; n = 111; Fig. 3.2). Furthermore, nestlings in non-delayed nests were more likely to recruit locally than their delayed counterparts if they fledged from nests that were initiated early (β = 1.197 ± 0.389; n = 106), but this was not the case for late-initiated nests (β = -0.018 ± 0.263; n = 115; Fig. 3.2). Although the pattern within early and late clutch initiation periods was the same between sites, the apparent seasonal increase in recruitment index for nestlings in delayed nests was driven by higher recruitment of this cohort at SDNRA as there was no difference in recruitment index of nestlings in delayed boxes at PG regardless of timing of clutch initiation.

The second-ranked model indicated that both delay treatment and the difference in actual from the intended brood size were important predictors of recruitment index. This model confirmed that nestlings in delayed nests were less likely to recruit locally (β = -0.461 ± 0.198) and that, in general, the likelihood of producing at least one recruit increased with larger positive differences in brood size from intended brood size (i.e., generally larger broods; β = 0.272 ± 0.112). Although larger positive differences between intended and actual brood sizes resulted in a greater probability of producing a recruit, the proportion of nestlings within a nest that fledged and recruited locally (PROC GLM) did not differ depending on differences between intended and actual brood sizes (i.e., the same proportion of the brood recruited regardless of brood size; β = 0.003 ± 0.003).

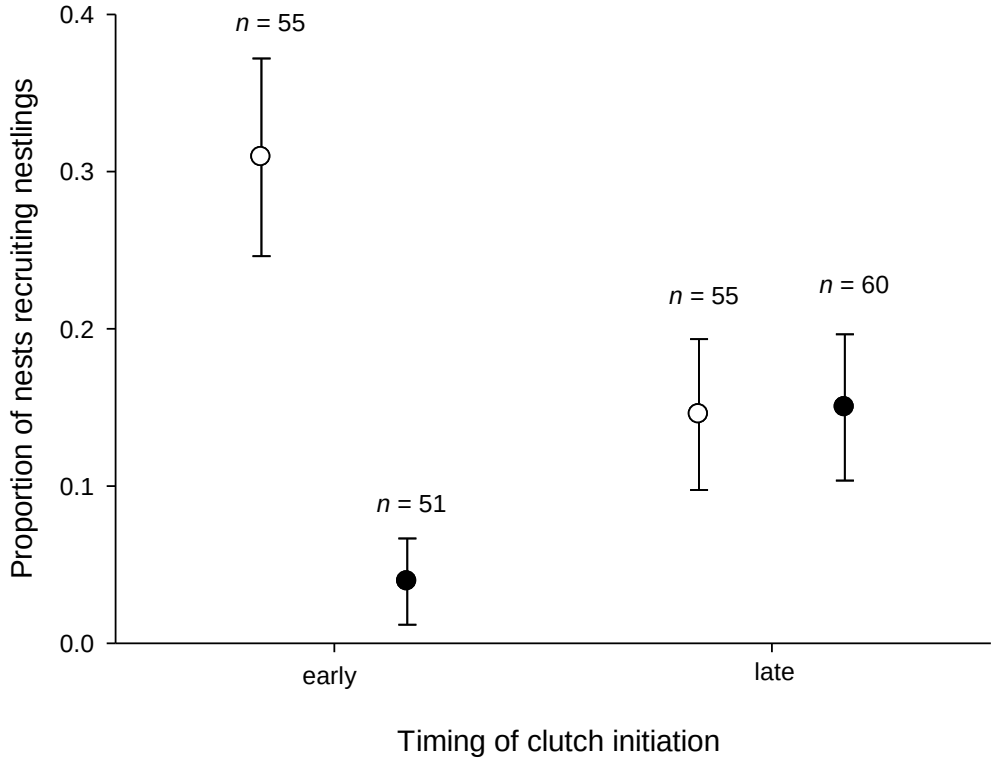


Fig. 3.2. Proportion (± SE) of nests recruiting nestlings for which hatching was delayed (closed circles) or not (open circles), by timing of clutch initiation (early, late) at the St. Denis National Research Area, Saskatchewan, and Prince George, British Columbia, 2008-09. Early timing represents nestlings produced by parents that initiated earlier than the median clutch initiation date, late timing represents nestlings produced by parents that initiated equal to or later than the median clutch initiation date. Number of nestlings (n) shown for each group.

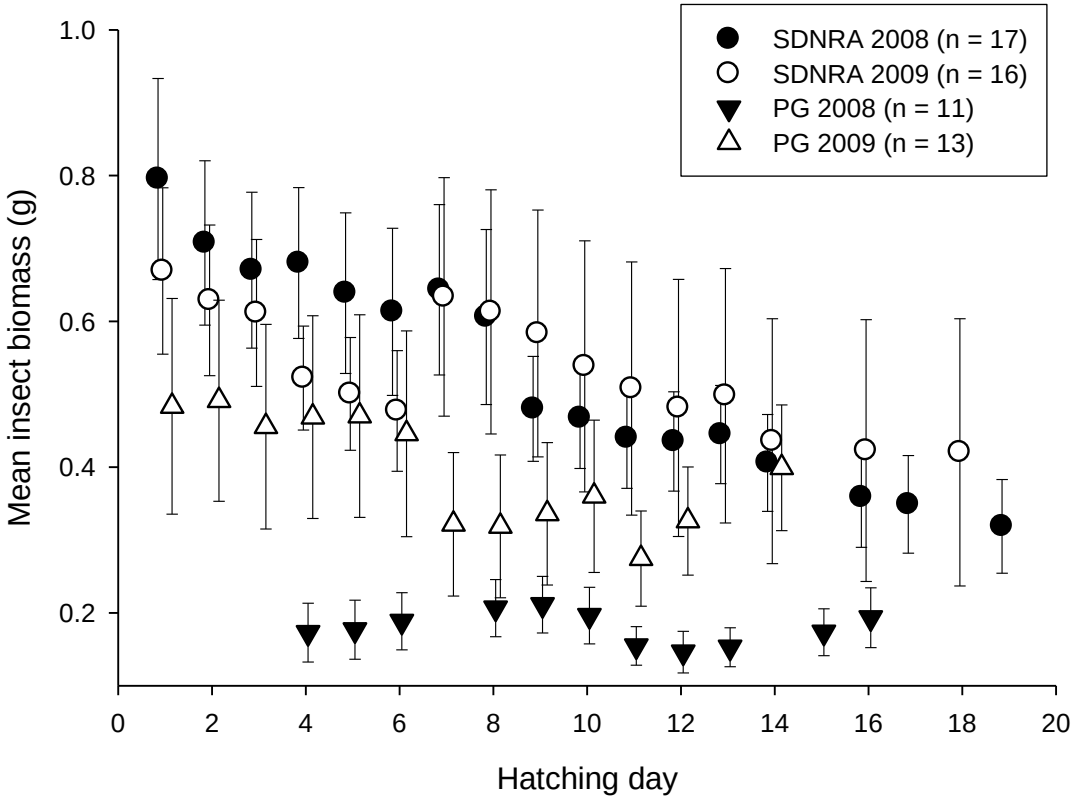


Fig. 3.3. Mean (±SE) insect biomass (g; averaged from when nestlings were 2-16 days-old for each hatching day) in relation to hatching day (day 1 represents the first day of nestling emergence within each site during each year) during the breeding season at the St. Denis National Research Area, Saskatchewan (SDNRA) and Prince George, British Columbia (PG), 2008-09. Number of hatching dates (n) is shown for each site and year.

3.4 DISCUSSION

I found that reduced reproductive success of late-breeding individuals was casually related to a seasonal decline in environmental quality. Several indices of nestling quality were linked to insect biomass, a resource that decreased with later hatching dates at both SDNRA and PG in both years (Fig. 3.3). Although my findings do not preclude potential additional effects, such as those of seasonally varying parasite loads (but see Harriman et al. 2014), the seasonal deterioration of the environment was strongly associated with declining food resources or less food per chick, resulting in lower quality nestlings. Indeed, multiple experimental tests which failed to control for parental quality

have documented support for the date hypothesis and have invoked indirect evidence to support declining food abundance as a principle aspect of the deteriorating environment (Norris 1993, Dawson 2008, Öberg et al. 2013).

There was little indication that early-nesting parents raised better quality nestlings than did late-nesters, although nestlings were in better body condition and were heavier at 16-days-old when raised by females in better body condition. While these findings suggest that female quality is an important predictor of some indices of nestling quality, body condition of females did not decrease seasonally and thus results are not consistent with predictions of the parental quality hypothesis. Nestlings in delayed nests were in poorer body condition and lighter than their non-delayed counterparts, possibly due to decreased abundance of food resources later in the season. Delay treatment and insect biomass were correlated, so parents with delayed hatching generally raised nestlings during periods of lower insect biomass.

Declining insect biomass and brood size enlargement resulted in nestlings that were lighter, in poorer body condition, had shorter head-bills, shorter and slower growing ninth primary feathers and less likely to survive to fledge. My results imply fitness-related costs of seasonally diminishing food supply for late-breeding individuals. Nestling tree swallows do not attain adult primary feather lengths while in the nest. Because insect biomass decreased seasonally, nestlings with shorter ninth primary feathers were more likely to be late-hatching individuals and thus were doubly disadvantaged as late-hatching nestlings may also have less time for feather growth prior to migration (O'Brien and Dawson 2008). Furthermore, skeletal growth of tree swallows is often completed by day 16 (Wiggins 1990, McCarty 2001), indicating that ontogenetic effects of food supply are permanent (Potti and Merino 1996). Finally, analyses of long-term data indicate that body mass of nestlings is an important predictor of first-year survival, with heavier nestlings being more likely to recruit locally than lighter nestlings (Shutler et al. 2006, Chapter 4).

I did not find that nestlings in reduced broods were of better quality than control nestlings despite evidence that nestlings in experimentally reduced broods receive more food per capita (Shutler et al. 2006). Siikamäki (1998) demonstrated that nestling pied flycatchers (*Ficedula hypoleuca*) raised in nests with delayed hatching were lighter at fledging and, moreover, showed that supplementally fed, delayed nestlings were similar

in mass to their non-delayed counterparts. In my study, clutch sizes of parents attending reduced broods were slightly larger than those in control and enlarged broods, presumably by chance alone, and this resulted in a smaller difference in brood sizes between reduced and control nests when compared with enlarged and control nests. This may explain why indices of nestling quality in reduced broods were not different from those in control broods.

Past research on tree swallows indicates that brood size manipulations can be used to effectively alter per capita provisioning rates to nestlings (McCarty 2002) and that nestlings in reduced or enlarged broods generally receive more or less food, respectively, than control counterparts (Shutler et al. 2006, Bortolotti et al. 2011). Although brood size manipulations provided an experimental framework for testing food abundance as a mechanism of deteriorating environmental conditions, measurements of insect biomass provided an opportunity to examine seasonal variation in food supply and to address potential interactive effects of food supply and treatments. Indeed, a well-supported model suggested that nestlings in enlarged broods were lighter than those in control and reduced broods, but only at low levels of insect biomass. These results indicate that the cost of raising enlarged broods depends on environmental conditions during the nestling period. Likewise, in a six-year brood size manipulation study of collared flycatchers (*Ficedula albicollis*), nestling condition was lower in experimentally enlarged broods and this effect was more pronounced in years with less food (Török et al. 2004). These findings underlie the importance of directly evaluating relationships between indices of environmental quality and fitness-related traits, and annual fluctuations in these indices, when assessing the implications of late breeding.

Enlarged broods of tree swallows produced more fledglings (Shutler et al. 2006), yet this relationship may be affected by food supplies, with a greater number of fledglings produced from enlarged broods in food-rich years and a threshold in the number of fledglings produced occurring in average food years (Török et al. 2004). Similarly, my results suggest that nestling survival was higher during periods of greater insect biomass. Furthermore, I detected a cost of enlarged brood sizes in the form of nestling mortality, independent of food abundance. Nestling survival was lower at PG than SDNRA possibly due to overall lower food supplies at PG (Fig. 3.3); however, this and a previous study

(Harriman et al. 2014) suggest that parents at PG are in poorer body condition than those at SDNRA, which may also account for these results.

Interestingly, in 2008 at SDNRA and PG, feeding rates by parents did not vary with insect biomass (Bortolotti et al. 2011), suggesting that changes in parental provisioning rates did not contribute to observed declines in nestling quality with declining food supply. The difference in mean insect biomass between PG and SDNRA was greater in 2008 than 2009 (Fig. 3.3), but despite these site differences, parental provisioning rates did not differ between SDNRA and PG in 2008 (Bortolotti et al. 2011). It is therefore unlikely that the relationship between insect biomass and nestling quality was driven by differential feeding rates in 2009 alone. Yet short-term measurements such as those conducted by Bortolotti et al. (2011) may not have been representative of the total parental provisioning effort for the duration of the nestling period. Insect abundance and parental provisioning behaviour may be negatively affected by weather conditions such as rainfall (Tinbergen and Dietz 1994, Dawson and Bortolotti 2000) and cooler temperatures (Winkler et al. 2013). Late-hatched nestlings experienced greater amounts of rainfall than early-hatched nestlings in 2008 (Harriman et al. unpubl. data) and parental provisioning rates were not measured during periods of rainfall (Bortolotti et al. 2011). Thus it seems likely that parents of late-hatching nestlings would be required to feed at greater rates during rain-free periods to fully compensate for frequent periods of interrupted or reduced provisioning. Finally, while adult provisioning rates may be a good index of the amount of food delivered to broods by parents (McCarty 2002), seasonal decreases in either food quality or amounts delivered per visit could explain for my results.

Recruitment of offspring is generally higher when nestling are raised during periods of greater food supply (Török et al. 2004). A fitness-related cost of the delay treatment was reflected in reduced local recruitment of nestlings in delayed nests of early-initiating parents when compared to their non-delayed counterparts. Early-initiating delayed parents actually produced fewer recruits than parents that initiated late. This may indicate that costs associated with early breeding are alleviated by environmental conditions during the nestling period. In particular, costs associated with egg formation are greater earlier in the season when food supplies are generally lower and temperatures

are cooler (Nilsson 1994, Perrins 1996, Schaper and Visser 2013). Costs of early laying may be outweighed by the benefits of raising offspring when food is more abundant (i.e., when intended) for early-breeding individuals, thus when these individuals are forced to raise offspring during periods of lower food abundance (i.e., later than intended), early-breeding individuals are not able to compensate for these costs, subsequently passing them onto nestlings. My finding that recruitment was lower for individuals for which hatching was delayed is similar to those who have used clutch removal and re-laying (Barba et al. 1995, Verhulst et al. 1995, Svensson 1997, Verboven and Visser 1998) and cross-fostering (Norris 1993) manipulations to induce changes in timing of nestling rearing. There was no difference in the likelihood of producing at least one recruit between late-initiating delayed and non-delayed parents. This is my only result that provides support for predictions of the quality hypothesis (see also Brinkhof et al. 1997) and indicates that effects of parental quality on offspring recruitment may be more important for late-initiating individuals. However, it is important to note that the span of hatching dates was greater for late than early-initiating parents due to the pattern in timing of clutch initiation (i.e., the distribution of clutch initiation dates is skewed to the right): very few delayed and non-delayed early-initiating parents overlapped in hatching date (and thus environmental conditions), whereas a greater number of late-initiating delayed and non-delayed parents did, and thus experienced similar environmental conditions.

The greater number of late-initiating delayed and non-delayed parents raising offspring during the same environmental conditions, along with the small number of nests producing recruits, may explain why late-initiating parents attending both delayed and non-delayed broods appeared to produce the same number of recruits. Parents that raised more nestlings than they intended (and thus generally having larger brood sizes) were more likely to produce a recruit (see also Török et al. 2004, Shutler et al. 2006). In general, delayed parents raised fewer nestlings than their non-delayed counterparts, suggesting that the observed differences in recruitment between delayed and non-delayed early-initiating individuals may be driven by brood size differences. However, subsequent analyses revealed that this was not the case and the pattern remained after accounting (separately) for brood size or the difference between intended and actual

brood size. It is important to note that the local recruitment index measures return rate and does not take into account natal dispersal rates, which could have been greater for later-hatched nestlings than their earlier-hatched counterparts. However, past research on tree swallows suggests that this is unlikely (Winkler et al. 2005).

The method of delaying hatch via egg storage provided the advantage of returning eggs to the female that laid them, which was particularly important in this context as egg quality, which has subsequent effects on offspring quality, varies with female quality and/or clutch initiation date (Risch and Rohwer 2000, Ardia et al. 2006b). However, like all experimental techniques employed to manipulate timing of breeding (see Verhulst and Nilsson 2008), egg storage has disadvantages. By necessity, this technique resulted in extended incubation duration for delayed parents and increased costs to delayed individuals could increase the likelihood of supporting predictions of the date hypothesis. I did not detect a cost of extended incubation on female or male body condition (see also Siikamäki 1995, Wiggins et al. 1998, Shutler et al. 2006). Furthermore, Bortolotti et al. (2011) noted no difference between provisioning rates of delayed and non-delayed parents irrespective of brood size. Although it is feasible that there were undetected costs on parental quality (e.g., immunocompetence) I suspect that costs of extended incubation to parents was minimal. It is also plausible that egg storage had a detrimental effect on embryo quality (Verhulst and Nilsson 2008); however, I detected no differences in nestling mass at 4 days of age in delayed and non-delayed nests.

Egg storage resulted in reduced egg hatchability, which subsequently resulted in smaller brood sizes in delayed nests when compared to non-delayed nests. Smaller brood sizes could have alleviated costs of raising offspring during periods of poor environmental conditions, leading us to mistakenly support predictions of the quality hypothesis. Nonetheless, few of my results were consistent with predictions of the quality hypothesis (recruitment of nestlings of late-initiating parents only), and non-delayed parents raised nestlings that were heavier and in better body condition than parents attending delayed broods. It is possible that differences in quality between delayed and non-delayed nestlings would have actually been larger had brood sizes been the same.

Timing of breeding is strongly associated with fitness (Daan and Tinbergen 1997b) and knowledge of what drives seasonal variation in fitness-related components,

such as reproductive success, is important for making inferences about consequences of altering breeding time on population dynamics, particularly in the context of effects of landscape and climate changes (Both and Visser 2001). Experimental tests of drivers of deteriorating environmental conditions are rare, and I am aware of only one such study that explicitly tested the mechanism of declining food abundance while controlling for parental quality (Siikamäki 1998) - despite the considerable attention this possible mechanism has received since the publication of the seminal paper by Perrins (1970). I accounted for parental quality and manipulated food availability on a per capita basis, while simultaneously considering indices of parental and environmental quality on two study sites over two breeding seasons. Therefore, I believe that my study provides strong evidence for the importance of food resources in mediating seasonal declines in avian offspring quality and survival. These findings have important implications for population dynamics of temperate-breeding insectivorous birds, for which food availability is intricately linked to local climatic conditions. Although experimental work has unveiled support for predictions of both the quality and date hypotheses on fecundity and offspring condition, studies of the putative effects of parental and environmental quality on first-year apparent survival are generally lacking, and thus are the focus of my next chapter.

CHAPTER 4: SEASONAL VARIATION IN FIRST-YEAR SURVIVAL OF TREE SWALLOWS (*TACHYCINETA BICOLOR*): EFFECTS OF PARENTAL QUALITY, LOCAL ENVIRONMENTAL CONDITIONS AND GLOBAL CLIMATE INDICES.

4.1 INTRODUCTION

How individual organisms respond to and interact with their environment produces variation in fitness among individuals. One key decision individuals in all environments must make is when to reproduce, a decision based on trade-offs involving a variety of factors including environmental cues and an individual's physiological condition. For organisms in seasonal environments, timing of reproduction is a critical

factor influencing fitness (reviewed in Chapter 3). Early breeding individuals regularly attain higher fitness than their late breeding counterparts (e.g., Kelly and Levin 2000, Varpe et al. 2007, Uller and Olsson 2010). Two primary hypotheses have been proposed to explain lower reproductive success of late breeders. The quality hypothesis predicts that higher quality individuals (phenotypic quality or condition) breed earlier in the season and that declining reproductive success among late breeders is associated with the difference in quality of territories used by early and late breeders and/or poor performance by late-breeding, lower quality individuals (Price et al. 1988, Verhulst and Tinbergen 1991). Alternately, the date hypothesis predicts that environmental quality declines seasonally and that the observed pattern in reproductive success is causally related to timing of breeding and thus affects all individuals in the same way (Perrins 1970).

Timing of breeding has been extensively studied in avian populations (reviews in: Arnold et al. 2004, Verhulst and Nilsson 2008), with seasonal variation in reproductive success being attributed to two primary patterns: declines in clutch and brood sizes with later breeding date and declining first-year survival of offspring hatched later in the season (Svensson 1997). A recent study suggests that declines in recruitment of offspring is the greatest contributing factor to lower fitness of late breeders (Öberg et al. 2013), yet comprehensive investigations of potential drivers of variation in first-year apparent survival (and thus accounting for recapture probability) of avian offspring is generally lacking.

Although experimental work has substantiated predictions of both the quality and date hypotheses on fecundity and offspring condition, studies of parental and environmental quality on return rates of offspring have found overwhelming support for the date hypothesis (review in Verhulst and Nilsson 2008). The one exception involved a study of Eurasian coots (*Fulica atra*) where offspring raised late in the breeding season by early-initiating parents attained apparent survival probabilities similar to offspring raised early in the season by early-initiating parents (Brinkhof et al. 1997). While experimental studies provide more rigorous tests of specific hypotheses, obtaining long-term experimental data is informative but costly. Correlative analyses of long-term data provide valuable insights into major drivers of temporal and spatial demographic

variation (Reid et al. 2008). Variation in demographic rates is likely linked to both large-scale processes such as winter climate that affect many individuals in a population and small-scale factors like spring weather conditions that influence individual life-histories (Coulson et al. 2001, Reid et al. 2008). Furthermore, both large-, small- and individual-scale effects should be considered simultaneously, although this has been generally rare due to the lack of availability of individual-scale information in long-term data sets (Reid et al. 2008).

In this study, I examined seasonal variation in first-year apparent survival of tree swallows (*Tachycineta bicolor*) at two distinct breeding locations in Canada, the St. Denis National Research Area, Saskatchewan (SDNWA) and Prince George, British Columbia (PG). I used mark-recapture data (1991-2010 at SDNRA and 2001-2010 at PG) to investigate the relative influence of large-, small- and individual-scale factors associated with the quality and date hypotheses on offspring survival in a comprehensive manner. Tree swallows are aerial insectivores, a guild of birds experiencing population declines throughout much of North America (Nebel et al. 2010, Shutler et al. 2012). In addition to being one of few studies to assess factors associated with first-year apparent survival in a migratory songbird, to my knowledge this is the first study to investigate first-year apparent survival in an aerial insectivore and as such findings may have particular value in providing insight into potential limiting factors in these populations.

4.2 METHODS

4.2.1 Study areas

Research was conducted on tree swallows nesting in nest boxes at two widely separated locations. The Saskatchewan site was the 385 ha St. Denis National Research Area (SDNRA; 52^{o}N, 106^{o}W), located about 40 km east of Saskatoon. This site had few trees and was within an agricultural landscape composed of alfalfa (*Medicago sativa* L.) and brome grass (*Bromus inermis* Leyss) cover, agricultural crops and abundant wetland basins. The depths of ponds in two semi-permanent wetland basins (pond 25 and pond 67), were measured in May and July, 1991-2012, following Conly et al. (2004).

Nest boxes at SDNRA were attached to a metal post 1.5 m above ground with the box entrance facing southeast; boxes were placed ~30 m apart. Boxes were first placed on this site in 1990 and the number of boxes increased until 1993, with varying numbers of boxes throughout the study (Table A1.1); box occupancy approached 100% during 1992-2012 (also, Shutler et al. 2012). Analyses of apparent survival at SDNRA included individuals that hatched 1991 – 2010 and were recaptured 1992 – 2012 as the majority (81%) of tree swallow recruits were detected within two years of hatching (37% were encountered the year after hatch).

Data were collected on two sites (both referred to as 'PG') in the vicinity of Prince George, British Columbia (53^{o}N, 122^{o}W). Exploratory analyses suggested no difference in apparent survival of fledglings between PG sites and thus data were combined for subsequent analyses. These sites were within open agricultural habitat interspersed with small stands of deciduous and coniferous trees and were within 30 km of each other. Nest boxes were placed in a continuous series ~30 m apart and mounted on wooden fence posts. Boxes were first erected at PG in 2001, with the subsequent addition of boxes throughout the study (Table A1.1); box occupancy was 46.6% at PG sites. Analyses of apparent survival at PG included individuals that hatched 2001 – 2010 and were recaptured 2002 – 2012. Sixty-two percent of individuals recruited the year after hatch, and by the second year, 96% of individuals that recruited locally were encountered.

4.2.2 Nest monitoring and nestling and adult measurements

Nest boxes were visited every 2 days beginning in early May until an egg was laid (clutch initiation date), and thereafter nests were visited daily to determine clutch size and onset of incubation. When laying was complete at a box, visits ceased until 2 days prior to the estimated date of hatch (12 days after the last egg was laid); thereafter nests were visited daily to determine the date of first nestling emergence and hatching success.

When all viable eggs had hatched, parents were captured in the box and either marked with an aluminum leg band or the existing band number was recorded. Mass (nearest 0.5 g measured with a 60 g spring scale) and length of wing (nearest 0.5 mm

with a ruler) were recorded each year. Other structural measurements were collected in some years but not others at each site (length of head-bill, etc.). Adults were sexed via the presence of a brood patch (female) or cloacal protuberance (male). Adult females were aged in the field as either second-year (SY) or after-second-year (ASY) using plumage characteristics (Hussell 1983). All un-banded adult males captured for the first time were recorded as after-hatch-year (AHY) because SY and ASY males are indistinguishable. Very few breeding adults evaded capture each year due to the strong recapture effort, except in 1993 and 1994 at SDNRA. Recapture rates were low in 1993 due to an extreme weather event that killed most nestlings so adults did not enter nest boxes to feed nestlings and could not be captured (Shutler and Clark 2003). Although estimates of apparent survival of nestlings from 1991 and 1992 may have been influenced by lower recapture effort, relatively few nestlings fledged in these years.

Nestling age was calculated by denoting the first day a nestling was present in the nest as day 0; therefore, all nestlings in a box were assigned the same age. Individual chicks within a nest were uniquely marked with aluminum bands at 12 (SDNRA) and either 12 or 16 (PG) days of age. Measurement of mass (nearest 0.25 g measured with a 30 g spring scale) was recorded for each nestling at 12 days-old at both sites. Nests were visited ~22 days post-hatch to determine fledging success. If nestlings were still present, subsequent visits were made every 2 days.

4.2.3 Data analysis

Due to differences in data availability, sites were considered separately. Because different experiments were conducted on both sites (e.g., Chapters 2 and 3; also Shutler et al. 2006), three data sets were compiled to test the appropriateness of including nests, nestlings or parents subjected to various experiments. The *unrestricted* data set included all fledglings except those that likely experienced reduced apparent survival as a result of experimentation (i.e., hatching delay experiments, Chapter 3). The *restricted* data set included all fledglings except those involved in experiments that could possibly influence apparent survival (i.e., brood size manipulations, Shutler et al. 2006). In the *highly restricted* data set I removed fledglings involved in all experiments, including those that I

did not suspect would influence apparent survival probability (i.e., exchanging eggs between nests).

I used Cormack-Jolly-Seber (CJS) models in Program MARK (White and Burnham 1999) to estimate first-year apparent survival probability (ϕ) of tree swallows, herein referred to as "apparent survival", as I cannot distinguish between mortality and natal dispersal (i.e., permanent emigration), which may be high (Hosner and Winkler 2007). In addition to estimating ϕ, CJS models calculate recapture probability (p). Notation of CJS models follows Lebreton et al. (1992). First, I examined temporal variation in ϕ and p by assessing 8 *a priori* models each for SDNRA and PG. These models varied from those with fully time-dependent (t, i.e., separate ϕ and p for each year) to time-constant models (i.e., ϕ and p remained constant over time). I selected the most appropriate time-specific model for each site and data set using AIC_c (see below) and then developed *a priori* sets of 55 (SDNRA) and 52 (PG) candidate models to examine relationships between indices of environmental and parental quality on ϕ (covariates discussed in detail below). Also, null and global models and 6 (SDNRA) and 7 (PG) interactions were considered. I subsequently examined the effect of annual occupancy rates of nest boxes and adult ϕ (SDNRA only) on p of fledglings by incorporating these covariates into best-approximating models explaining ϕ. Relationships between covariates were explored using Pearson correlations (PROC CORR), analyses of variance (PROC GLM), and linear mixed models (PROC MIXED) when appropriate using SAS (SAS Institute Incorporated 2009). Strongly correlated covariates ($r \geq 0.7$) were not included in the same model, but were incorporated into alternate models.

I used an information-theoretic approach (Akaike's Information Criterion adjusted for small sample size; AIC_c) to examine the relative support for models about variation in ϕ (Burnham and Anderson 2002). A goodness-of-fit test was conducted on the highly parameterized global models using the median $\hat{c}$ method (Program MARK) and results suggested that model fit was good (e.g., data were not overdispersed) at SDNRA ($\hat{c}$ = 1.028, SE = 0.024) and PG ($\hat{c}$ = 1.004, SE = 0.007). Within each candidate set, a model with the smallest AIC_c value was considered the most parsimonious, but models within 4 AIC_c units of the best-approximating model ($\Delta AIC_c < 4$) were considered plausible

(Burnham and Anderson 2002). The estimates of the likelihood of the model relative to competing models (Akaike weight; ω_i) were also used to make inferences. Unless otherwise stated, parameter estimates of the most parsimonious model ($\beta \pm$ SE) and the model-averaged estimates of ϕ and p obtained from all models ($\beta \pm$ unconditional SE) are reported (Burnham and Anderson 2002).

4.2.4 Quality hypothesis

Four covariates were used to index parental quality: minimum age, prior breeding site experience and body mass of the female parent, and clutch size (Table A2.1). Nonlinear relationships were also examined for each covariate except prior breeding site experience. Older parents are generally considered to be of higher quality than their younger counterparts and often attain higher reproductive success and produce more recruits in avian species (Forslund and Pärt 1995, Robertson and Rendell 2001, Blums et al. 2002). Furthermore, individuals with prior breeding site experience may attain higher reproductive success irrespective of their age (Saunders et al. 2012). I predicted that offspring would have higher ϕ when produced by adults that had previously bred in the colony and/or were older. Furthermore, high-quality females, or females with access to more resources, may lay larger clutches (Winkler and Allen 1996, Pettifor et al. 2001, Schoech et al. 2008). Thus, I predicted ϕ would be higher for individuals raised by females that laid larger clutches.

For previously unmarked adults, I assumed the first capture period coincided with an individual's first breeding attempt at that site and that the individual was likely 1 or 2 years of age (details below). Prior breeding site experience and adult minimum age were determined based on each bird's mark-recapture history. Prior breeding site experience was a binary covariate. Upon capture an adult was either unmarked and assumed to be an inexperienced breeder at that site, or banded and an experienced breeder. I used information for the year an individual was marked to calculate adult minimum age (see also Murphy 2007). Adult males captured in the breeding colony for the first time were assigned a minimum age of 1-year-old. Likewise, females were either assigned an age of 1 (if SY) or 2 years old (if ASY). If an adult hatched in the colony, its exact age was

known. Adult minimum ages ranged from 1 - 10 at SDNRA and 1 - 7 at PG, although the majority of breeding adults were designated as 1 (males) or 2 (females) years old at both sites. Due to the small number of older birds, I grouped these individuals in as being either >4 years old or >5 years old based on frequency distributions and subsequently evaluated these groupings for model fit. At both sites, models with adults >4 years old grouped together were better supported and used in final analyses. Due to the obvious association between breeding site experience and parent minimum age, these covariates were not included in the same models.

Body size of adults could also reflect parental quality. For instance, larger adults could have higher return rates (Guillemain et al. 2013) and arrive earlier on the breeding grounds (Dittmann and Becker 2003, Smith and Moore 2005, Matyjasiak et al. 2013), so I predicted that larger individuals would produce offspring with higher ϕ. I examined the strength of relationships between ϕ and parent body mass, length of wing and body condition in exploratory analyses of *unrestricted* datasets. Residuals of adult mass regressed against length of wing and nestling age when the adult was captured were used as an index of adult body condition (O'Brien and Dawson 2013). Analyses suggested that body mass of parents was a better predictor of ϕ than body condition index or length of wing at SDNRA and indices were equivalent at PG. Quadratic nonlinear models were not well supported. Some individuals were missing measurements of wing length, and thus to maintain sample sizes, only parent body mass was considered in subsequent analyses.

At SDNRA and PG, exploratory analyses of the *unrestricted* data set (and restricted to parents captured within 4 days of hatch) revealed that female and male body masses were correlated, suggesting assortative mating by size among breeding pairs. At SDNRA (n = 1081 pairs) and PG (n = 626 pairs), mixed effects models indicated that male body mass (SDNRA, $\beta = 0.158 \pm 0.027$; PG, $\beta = 0.154 \pm 0.035$) and male minimum age (SDNRA, $\beta = 0.123 \pm 0.037$; PG, $\beta = 0.295 \pm 0.040$) were positively correlated with female body mass and minimum age, respectively, after accounting for random effects of year (PROC MIXED). Furthermore, models including indices of female quality (body mass, minimum age), were better supported in their effect on ϕ than were similar indices of male quality in preliminary analyses. Male tree swallows are often more challenging to capture than females, and thus there are more missing values associated with male

parents. To maintain sample size, and because of positive associations between male and female quality, I only included female parents in analyses. Finally, to account for changes in body mass related to timing of capture relative to the hatching date of chicks, residuals derived from regressions of female mass against age of nestlings for each site were used in subsequent analyses.

4.2.5 Date hypothesis

Studies focusing on climate impacts on juvenile survival and recruitment rates are rare (Jenouvrier 2013), yet these demographic components of population dynamics are likely to be more affected by climate variation than adult survival probability (Sandvik et al. 2012, Jenouvrier 2013). Most studies of the effects of climate on components of fitness documented indirect effects of climate through habitat availability or food resources, but direct effects of climate may also exist (Jenouvrier 2013). Furthermore, climate effects may be non-linear due to physiological and ecological constraints and/or thresholds (Grosbois et al. 2008, Jenouvrier 2013). Three categories of covariates were considered as indices of environmental quality: large-scale climate factors, and small-scale local indices of moisture and, at SDNRA only, wetland depth (Table 4.1). Warmer conditions have been associated with higher parental (Dybala et al. 2013a) and first-year (Stokke et al. 2005, Reid et al. 2008) survival probabilities in birds. Wet conditions on the wintering (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005, Mihoub et al. 2010, LaManna et al. 2012) and breeding (Dybala et al. 2013a; RGC et al. unpubl. data) grounds have been linked to survival in birds, likely as a result of increased food abundance during wet years. Thus I predicted that ϕ would be associated with warmer conditions year-round and wetter conditions on the breeding and wintering grounds. However, ϕ may be highest under average conditions, or a threshold may exist when it becomes "too wet," so nonlinear relationships were also considered. Although these covariates are annual measurements of environmental quality rather than within-season metrics, they may provide insight into seasonal conditions within each year and I may expect interactions between date-related covariates (e.g., wetland depth) and clutch initiation date as predictors of ϕ. For example, food abundance may not be limiting

during wet years and thus I would not expect to observe a seasonal decline in ϕ during these years, whereas food may be more limiting in dry years when I may expect a stronger seasonal decline in ϕ.

Past research has summarized specific climate indices during distinct periods of the annual life-cycle such as fall and spring migration and breeding and wintering periods (Grosbois et al. 2008, Balbontín et al. 2009, Franke et al. 2011) or spanning over multiple annual life-cycle events when a specific climatic factor is known to be strongest (Mazerolle et al. 2005, LaManna et al. 2012). Four global climate teleconnections may influence population dynamics of tree swallows, for which I selected 5 indices: North Atlantic Oscillation (NAO), Southern Oscillation Index (SOI), Bivariate ENSO Timeseries (BEST), Pacific Decadal Oscillation (PDO), and Pacific-North American (PNA) teleconnection index. Monthly estimates for each index were obtained from the National Oceanic and Atmospheric Administration (NOAA Climate Prediction Center 2013).

The climate effects of NAO are strongest in the winter and typically influence patterns in temperate North America and Europe. Positive NAO values generally correspond with warmer temperatures in the wintering range of tree swallows, and climate patterns produced by NAO are typically strongest in eastern North America. El Niño Southern Oscillation (ENSO) is an ocean and atmospheric phenomenon which results in generally warm (El Niño) or cold (La Niña) periods that cycle every 2 – 7 years. In western Canada, and thus on the breeding grounds of swallows in this study, El Niño periods are generally warmer (Shabbar and Khandekar 1996) and drier (Akinremi et al. 2001, Brigode et al. 2013) than average. El Niño phases are associated with wetter conditions throughout much of the southern United States, including California, and in northern Mexico throughout the year, although the effects are generally greatest during the winter months (Kurtzman and Scanlon 2007, Tourigny and Jones 2009). Conversely, El Niño phases are associated with drier conditions in Florida and along the southern edge of the Gulf of Mexico. Recent research suggests that, in general, adult tree swallows nesting at SDNRA over-winter near the Gulf of Mexico in the USA and Mexico, whereas adults nesting at PG over-winter in northwestern Mexico (D. Bradley, University of Guelph, unpubl. data). The potential for different effects of ENSO on ϕ of tree swallows

nesting at SDNRA and PG lead to unique predictions during different annual life-cycle stages (Table A2.1). The SOI and BEST are two measures of ENSO. The SOI provides a measure of fluctuations in air pressure between the western and eastern tropics during El Niño and La Niña episodes. The BEST index combines SOI with sea surface temperatures in the tropical Pacific. For specific temporal and spatial predictions associated with the BEST index and SOI see Table A2.1.

The PNA and PDO produce ENSO-like patterns of Pacific climate variability. Unlike the shorter oscillation periods of the other climate cycles, the PDO generally fluctuates over bidecadal and multidecadal periods (Mantua et al. 1997). Effects of the PNA and PDO are strongest during the winter months (Leathers et al. 1991, Newman et al. 2003). Climate patterns produced by the PNA and PDO interact with those produced by ENSO (Kurtzman and Scanlon 2007, Younas and Tang 2013). In general warm (positive) phases of the PNA and PDO amplify the effects of El Niño events and cold (negative) phases of the PNA and PDO amplify the effects of La Niña events, so that a positive PNA or PDO effects during an El Niño year would produce particularly wet conditions in the southern United States and northern Mexico (Newman et al. 2003, Kurtzman and Scanlon 2007). Following LaManna et al. (2012), I calculated residuals of PNA and PDO regressed against either SOI or BEST and included residuals in additive models with SOI or BEST instead of the actual PNA or PDO values.

I calculated the mean effect of each climate index during time periods corresponding to distinct annual life-cycle events, as well as those spanning multiple periods (i.e., overwintering and spring migration). A total of 24 exploratory linear climate models were considered and non-linear (nonlin) relationships between well-estimated climate factors and ϕ were subsequently assessed (Grosbois et al. 2008). This preliminary screening was used to reduce the number of covariates for final modelling steps. Analyses of the SDNRA data set suggested that BEST_sumr (May – July; i.e., breeding season in year of hatch) and BEST_fall_nonlin (August – September; i.e., fall migration) were the strongest climate predictors of ϕ. At PG, SOI_sumr (May – July) and SOI_fall (August – September) were the best predictors ϕ and corresponded to climatic conditions during the breeding season and subsequent fall migration, respectively. At both SDNRA and PG, in models where BEST_sumr or SOI_sumr and BEST_fall or SOI_fall

(respectively) were substituted for each other, model ranking and estimates were equivalent, likely due to the high degree of correlation between ENSO during the summer and fall. Because I had other breeding season covariates, BEST_fall and SOI_fall rather than BEST_sumr and SOI_sumr were included in additive models at SDNRA and PG, respectively. Effects of climate indices that spanned the winter months were not well estimated at either site.

The Palmer Drought Severity Index (PDSI) is a local measure of relative dryness or wetness commonly used to predict droughts in the United States and Canada. The PDSI incorporates antecedent precipitation, moisture supply and moisture demand to measure the departure in atmospheric moisture supply and demand at the soil surface relative to local mean conditions (Palmer 1965). A PDSI value of 0 represents average moisture conditions where ≥ 4 and ≤ -4 represent extremely wet and extremely dry conditions, respectively. The Palmer moisture anomaly index (*Z* index) is used to calculate the PDSI and is a monthly measure of surface moisture anomaly that does not account for antecedent conditions. The Z index is more sensitive to short-term changes in soil moisture than PDSI (Karl 1986). A Z index value of 0 represents average moisture conditions where ≥ 3.5 and ≤ -2.75 represent extremely wet and extremely dry conditions, respectively. Monthly PDSI and *Z* values were obtained for SDNRA (station 4057165) and PG (station 1096453) from Agriculture Canada (2013). To my knowledge, the effects of PDSI and Z on ϕ of birds have not been previously investigated. At SDNRA, mean December – March PDSI was strongly correlated with May wetland depth (pond 67: $r = 0.763$, $P < 0.001$, $n = 20$) and thus these indices are likely highly suitable as an index of local moisture conditions on the breeding grounds. The PDSI and Z index are likely linked to food availability as aerial insect abundance is greater during relatively wet periods (Blancher and Robertson 1987, Fast 2007).

A total of 20 exploratory linear Palmer models (10 PDSI, 10 *Z* index for the same time periods) were considered and non-linear relationships between well-estimated covariates ϕ were subsequently assessed. Analyses suggested that PDSI directly prior to the breeding season (December – March) was the best Palmer-related predictor of ϕ at both SDNRA and PG. Nonlinear relationships were not well supported.

Deeper spring ponds are associated with early clutch initiation (Fast 2007) and higher ϕ of adult female tree swallows (RGC unpubl. data) at SDNRA. I assessed the relative influence of the depth of two semipermanent ponds (pond 25 and 67) in May and July on ϕ at SDNRA. I included linear and nonlinear terms, resulting in 8 models. The best predictor of ϕ at SDNRA was the May depth of pond 67.

4.2.6 Either hypothesis

I considered two covariates that could be consistent with predictions of both the quality and date hypotheses: clutch initiation date and nestling mass (Table 4.1). Because the quality and date hypotheses are not mutually exclusive, not only do I predict that covariates I previously assigned to the quality or date hypothesis to exhibit additive, or even interactive effects on ϕ, I also think that these two "combination covariates" are of primary interest as they are easily measured and often recorded in avian research. I predicted that ϕ would be higher for offspring produced by parents with earlier clutch initiation dates (Blums et al. 2002, Shutler et al. 2006) and for individuals that were heavier prior to fledging (Brinkhof et al. 1997, Shutler et al. 2006).

Clutch initiation dates were standardized so that day 1 represented the first clutch initiation within each year on each site (CID). In addition to CID, I considered relative clutch initiation date (RCID) which described whether parents initiated egg laying earlier (negative values) or later (positive values) than the median clutch initiation date for first attempts (day 0) at each site and in each year. RCID and CID are strongly correlated at both SDNRA ($r = 0.954$, $P < 0.001$, $n = 1912$) and PG ($r = 0.919$, $P < 0.001$, $n = 752$). However, I chose to consider both covariates in separate models because CID does not provide any context to aid in interpretation of the distribution of clutch initiation dates within a year, whereas RCID does.

Mass of nestling tree swallows peaks at ~12 days of age and varies relatively little between 10 and 14 days of age (Quinney et al. 1986; VBH et al. unpubl. data). Although most nestlings were measured at 12 days-old, there was some variation in age at measurement because nest visits were avoided during poor weather conditions. Nestlings measured before 10 days-old and after 14-days-old were removed from all analyses. Non-

linear relationships were investigated. Body mass of nestlings was moderately correlated with length of wing at SDNRA ($r = 0.335$, $P < 0.001$, $n = 10379$) and primary feather length at PG ($r = 0.447$, $P < 0.001$, $n = 3477$).

4.3 RESULTS

Descriptive statistics for covariates of interest and sample sizes at SDNRA and PG are show in Table 4.1. Furthermore, annual values of number of fledglings, recruits, number of nest boxes and occupancy rates are shown in Table A1.1. At SDNRA, 530 of 10380 nestlings were recruited based on the *unrestricted* data set, and 295 were male, 224 female and 11 were of unknown sex. At PG, 137 of 3479 nestlings recruited based on the *unrestricted* dataset, of which 60 were male and 77 were female.

Table 4.1. Descriptive statistics (mean or median ± standard deviation) for tree swallows (*Tachycineta bicolor*) on the St. Denis National Research Area, Saskatchewan (SDNRA), 1991-2010, and near Prince George, British Columbia (PG), 2001-2010. With the exception of the total number of fledglings and recruits, all means, medians and ranges are per year and are based on the *unrestricted* datasets for both sites.

	SDNRA	PG
total no. fledglings (range/year)	10380 (22 - 917; n = 20 years)	3479 (70 - 532; n = 10 years)
total no. recruits	530	137
mean recruits/year (range)	27.89 ± 18.19 (0 - 56); n = 20 years	13.70 ± 6.82 (2 - 25); n = 10 years
mean annual clutch initiation date of first clutches/year (range)	22 May ± 4.72 days (14 May - 31 May); n = 20 years	22 May ± 5.08 days (13 May - 29 May); n = 10 years
median annual clutch initiation date/year (range)	28 May ± 3.43 days (23 May - 5 June); n = 20 years	30 May ± 3.30 days (24 May - 4 June); n = 10 years
mean clutch size	6.33 ± 0.95 eggs (2 - 12 eggs); n = 1912 nests	5.97 ± 0.93 eggs (2 - 9 eggs); n = 752 nests
mean nestling mass	23.06 ± 2.08 g (10.00 - 29.50 g); n = 10380 nestlings	21.62 ± 2.19 g (10.75 - 27.50 g); n = 3479 nestlings
mean female mass	21.75 ± 1.68 g (16.00 - 29.00 g); n = 1912 individuals	19.78 ± 1.31 g (16.25 - 23.75 g); n = 752 individuals
mean proportion of unmarked females[a] captured/year (range)	0.49 ± 0.16 (0.32 - 1); n = 20 years	0.63 ± 0.19 (0.45 - 1); n = 10 years
mean Palmer Drought Severity Index (range)	0.25 ± 1.82 (-3.51 to 4.13); n = 20 years	2.35 ± 1.12 (0.655 to 4.805); n = 10 years
mean SOI_fall[b] (range)	0.003 ± 1.466 (-2.40 to 3.35); n = 20 years	0.24 ± 1.42 (-1.35 to 3.35); n = 10 years

[a] No prior breeding experience at study site

[b] Mean SOI August-September

4.3.1 Variation in apparent survival and recapture rates with time

The best-supported model at SDNRA suggested that (i) ϕ differed between the first (i.e., hatch-year to 1-year-old) and all subsequent intervals and (ii) *p* differed between the first, second and all subsequent intervals ($\omega_i = 0.703$). This model structure ($\phi_{age\ 1 +\ (.\ after)}$, $p_{occasion1 + occasion2 + (.\ after)}$) was used for all models evaluating the effect of covariates on ϕ. At PG, the most parsimonious model indicated that ϕ differed between the first, second and all subsequent intervals whereas *p* differed between the first and all subsequent occasions ($\omega_i = 0.415$). This model structure ($\phi_{age\ 1 +\ age\ 2 + (.\ after)}$, $p_{occasion1 + (.\ after)}$) was used for all models evaluating the effect of covariates on ϕ at PG.

Model rankings were similar between *unrestricted*, *restricted* and *highly restricted* data sets at both SDNRA and PG (Appendix 3). Furthermore, parameter estimates were similarly well estimated and followed the same pattern for the same models among data sets (Appendix 3). Therefore, results from modelling of the *unrestricted* data sets are reported.

4.3.2 Models incorporating covariate effects to explain apparent survival and recapture rates

At SDNRA, the top model explaining ϕ of tree swallows included nestling mass, the female parent's breeding site experience and an interaction between the Palmer Drought Severity Index and clutch initiation date (Table 4.2). All parameters were well estimated (Table 4.3). ϕ of tree swallows at SDNRA was higher for heavier nestlings (Fig. 4.1) and those produced by females with prior breeding site experience (Fig. 4.2). To examine the interaction between the PDSI and clutch initiation date, data were analyzed in two ways: covariates in the top model were included in analyses (1) for which early (> median) and late (≤ median) clutch initiation dates were separated and (2) separately for positive (relatively wet) and negative (relatively dry) PSDI values. ϕ increased with increasingly wet conditions for individuals from both early-initiated ($\beta = 0.187 \pm 0.036$; $n = 4257$) and late-initiated ($\beta = 0.078 \pm 0.035$; $n = 6123$) nests, and the difference in ϕ between these two cohorts was greatest during very wet conditions (Fig. 4.3). ϕ declined with later clutch initiation dates in both relatively wet ($\beta = -0.064 \pm$

0.026; n = 5624) and dry (β = -0.082 ± 0.033; n = 4756) years and overall ϕ was higher during years with positive PSDI values (Fig. 4.4). Model-averaged ϕ and p (ϕ = 0.080 ± 0.004; p = 0.221 ± 0.017) were virtually identical to those estimated by the best-approximating model (ϕ = 0.080 ± 0.004; p = 0.221 ± 0.017). I explored the effect of ϕ of parents and the proportion of boxes occupied on p for the top two models. Inclusion of percent occupancy (β = -3.289 ± 1.842) in the most parsimonious model slightly improved model fit (ω_i = 0.578) when compared to the model without (ω_i = 0.326) but reduced the precision of the estimate of the p and thus I did not consider this model further.

Wetter years corresponded to years with earlier first (r = -0.471, P = 0.036, n = 20) and median clutch initiation dates (r = -0.504, P = 0.023). Nestlings were also heavier in wetter years (r = 0.202, P < 0.001, n = 1912 nests), and the inclusion of this additive factor in the most parsimonious model suggested that the effect associated with the Palmer Drought Severity Index on ϕ was independent of nestling mass. Furthermore, fewer breeding females had prior experience at SDNRA in wetter years (PROC LOGISTIC; β = -0.078 ± 0.024, n = 1912). The mean Palmer Index prior to the breeding season (December – March) was not correlated with climate indices considered in final analyses, including ENSO during the breeding season (BEST May – July; r = 0.086, P = 0.718, n = 20).

After accounting for annual variation (random effect of year), recaptured female parents were heavier at hatch (β = 0.309 ± 0.068; n = 1912) but did not produce larger clutches (β = -0.079 ± 0.044) or heavier nestlings (β = 0.067 ± 0.068, n =10380; additional random effect of nest id) than females not previously captured in the colony (PROC MIXED; Table 4.4). Previously marked females also did not initiate clutches earlier relative to females not previously captured in the colony (β = -0.521 ± 0.315; PROC GLM; Table 4.4). Previously marked females were more likely to pair with previously marked males than unmarked males (β = 0.135 ± 0.064; n = 1083; PROC LOGISTIC).

There were multiple competitive models for explaining ϕ of tree swallows at PG (Table 4.2). All top models included clutch size, and those with the greatest ω_i included relative clutch initiation date. Estimates for these covariates were precise and ϕ was fairly

well estimated as judged by 95% confidence limits (Table 4.3). ϕ was higher for individuals of parents with relatively early clutch initiation dates but lower for fledglings produced by females laying larger clutches (Fig. 4.5). Despite the moderate negative correlation between relative clutch initiation date and clutch size (r = -0.460, $P < 0.001$, n = 555), additive models including both covariates received more support than models including only one of the covariates. Furthermore, although an interaction between relative clutch initiation date and clutch size is included in a plausible model (Table 4.2), all parameters for this model were poorly estimated, including the interaction term (Table A3.1). There was no evidence of a non-linear relationship between clutch size and ϕ. As predicted, after accounting for annual variation (random effect of year), heavier (β = 0.147 ± 0.027; n = 752), older (β = 0.253 ± 0.036) and recaptured (β = 0.299 ± 0.068) female parents laid larger clutches at PG. Brood sizes at hatch (β = 0.942 ± 0.035) and 12 days post-hatch (β = 0.832 ± 0.048) were larger in nests with larger clutches at PG. Furthermore, after accounting for random effects of year and nest id, nestlings from larger clutches tended to be lighter (β = -0.089 ± 0.060, n = 3479; PROC MIXED).

Other plausible models at PG suggested higher ϕ during El Niño years and for females with prior breeding site experience. However, parameters for SOI (β = -0.072 ± 0.065) and female breeding site experience (β = 0.182 ± 0.182) were imprecise. At PG, model-averaged ϕ and p (ϕ = 0.049 ± 0.005; p = 0.489 ± 0.051) were identical to those estimated by the best-approximating model (ϕ = 0.049 ± 0.005; p = 0.489 ± 0.051).

Table 4.2. Model selection for first-year apparent survival probabilities of nestling tree swallows (*Tachycineta bicolor*) at the St. Denis National Research Area, Saskatchewan (SDNRA), 1991-2010, and near Prince George, British Columbia (PG), 2001-2010. Only models with $\Delta AIC < 4$, the base time series-only (Null) and full parameterized (Global) models are presented.

Site	Model structure[a]	K[b]	-2logL[c]	AIC_c[d]	ΔAIC_c[e]	ω_i[f]
SDNRA	PDSI * CID + CID_nonlin + mass + fem_recap	11	7076.873	7098.896	0.000	0.773
	PDSI + CID + CID_nonlin + mass + fem_recap	10	7082.875	7102.895	3.998	0.105
	Global (PDSI + CID + CID_nonlin + mass + fem_recap + BEST_fall + BEST_fall_nonlin + fem_mass + clutchsz)	14	7080.441	7108.478	9.582	0.006
	Null	5	7150.279	7160.284	61.388	0.000
PG	clutchsz + RCID	7	1697.278	1711.309	0.000	0.152
	clutchsz + RCID + SOI_fall	8	1696.026	1712.065	0.756	0.104
	clutchsz + RCID + fem_recap	8	1696.279	1712.318	1.010	0.092
	clutchsz + CID	7	1698.587	1712.617	1.308	0.079
	clutchsz + RCID + SOI_fall + fem_recap	9	1694.911	1712.960	1.652	0.067
	clutchsz * RCID	8	1697.222	1713.261	1.953	0.057
	clutchsz + RCID + fem_mass + fem_recap	9	1695.519	1713.568	2.259	0.049
	CID	6	1701.875	1713.898	2.589	0.042
	RCID	6	1701.910	1713.933	2.624	0.041
	CID * PDSI	8	1698.029	1714.068	2.759	0.038
	CID + PDSI	7	1700.425	1714.455	3.147	0.032
	CID + fem_mass	7	1700.574	1714.605	3.296	0.029
	CID + fem_age	7	1700.739	1714.769	3.461	0.027
	CID + fem_recap	7	1700.994	1715.024	3.716	0.024
	RCID + RCID_nonlin	7	1701.128	1715.158	3.849	0.022
	CID + mass + PDSI	8	1699.256	1715.295	3.987	0.021
	Global (PDSI + CID + mass + fem_mass + fem_recap + SOI_fall)	11	1696.139	1718.210	6.901	0.005
	Null	5	1712.361	1722.377	11.069	0.000

[a] Factors included Palmer Drought Severity Index (PDSI), clutch initiation date (CID), the quadratic term of clutch initiation date (CID_nonlin), relative clutch initiation date (RCID), the quadratic term of relative clutch initiation date (RCID_nonlin), clutch size (clutchsz), nestling mass (mass), female breeding site experience (fem_recap), female mass (fem_mass), female minimum age

(fem_age), BEST index August-September (BEST_fall), the quadratic term of BEST index August-September (BEST_fall_nonlin), SOI August-September (SOI_fall), and a time-specific only model (null). Models with interactions (*) between factors also included the main effects.

[b] Number of estimable parameters.

[c] Deviance.

[d] Akaike's Information Criterion corrected for small sample size.

[e] Difference in AIC_c values between each model and the model with the lowest AICc value.

[f] Estimates of the likelihood of the model, given the data; normalized to sum to 1 (Burnham and Anderson 2002).

[g] Summarized by nest.

Table 4.3. Parameter estimates (on logit-link scale), standard errors (SE) and lower and upper 95% confidence interval limits (CI) from top-ranking model estimating first-year apparent survival of tree swallows (*Tachycineta bicolor*) at St. Denis National Research Area, Saskatchewan (SDNRA), 1991-2010, and Prince George, British Columbia (PG), 2001-2010.

Site	Parameter	Estimates	SE	Lower CI	Upper CI
SDNRA	ϕ: β_0	-3.913	0.537	-4.966	-2.860
	ϕ: β_{PDSI}	0.219	0.045	0.132	0.307
	ϕ: β_{CID}	-0.069	0.020	-0.109	-0.029
	ϕ: $\beta_{PDSI*CID}$	-0.011	0.005	-0.021	-0.002
	ϕ: $\beta_{CID\ nonlin}$	0.001	0.001	0.000	0.003
	ϕ: β_{mass}	0.073	0.022	0.030	0.117
	ϕ: β_{fem_recap}	0.216	0.095	0.029	0.403
	ϕ: β_2	0.491	0.066	0.362	0.621
	p: β_1	-1.259	0.098	-1.451	-1.067
	p: β_2	0.377	0.109	0.162	0.591
	p: β_3	0.891	0.118	0.660	1.122
PG	ϕ: β_0	-1.352	0.705	-2.734	0.030
	ϕ: $\beta_{clutchsz}$	-0.249	0.115	-0.475	-0.024
	ϕ: β_{RCID}	-0.069	0.020	-0.108	-0.031
	ϕ: β_2	0.361	0.255	-0.138	0.860
	ϕ: β_3	-0.140	0.170	-0.473	0.192
	p: β_1	-0.044	0.204	-0.444	0.356
	p: β_2	1.721	0.341	1.053	2.390

[a] Factors included Palmer Drought Severity Index (PDSI), clutch initiation date (CID), the quadratic term of clutch initiation date (CID_nonlin), nestling mass (mass), female breeding experience (fem_recap), relative clutch initiation date (RCID), and clutch size (clutchsz). Reported are parameter estimates (β) of first-year apparent survival probability (ϕ) and recapture probability (p), including intercepts of first-year apparent survival probability (β_0) and all subsequent intervals (β_2; SDNRA) or the second interval (β_2) and all subsequent intervals (β_3; PG) and intercepts of recapture probability for the first-interval (β_1) and all subsequent intervals (β_2; PG) or the second interval (β_2) and all subsequent intervals (β_3; SDNRA).

Table 4.4. Descriptive statistics (mean ± standard deviation) for adult female tree swallows (*Tachycineta bicolor*) with no prior breeding experience (unmarked) or with prior breeding experience (marked) on the St. Denis National Research Area, Saskatchewan, 1991-2010, based on the *unrestricted* dataset.

	Unmarked (*n* = 816)	**Marked (*n* = 1096)**
clutch initiation date	28 May ± 6.89 days	28 May ± 6.74 days
clutch size	6.37 ± 0.94 eggs	6.29 ± 0.96 eggs
residual body mass[a]	-0.166 ± 1.454 g	0.143 ± 1.469 g
nestling body mass	22.99 ± 1.75 g	23.08 ± 1.79 g

[a] Regressed against nestling age when female was captured

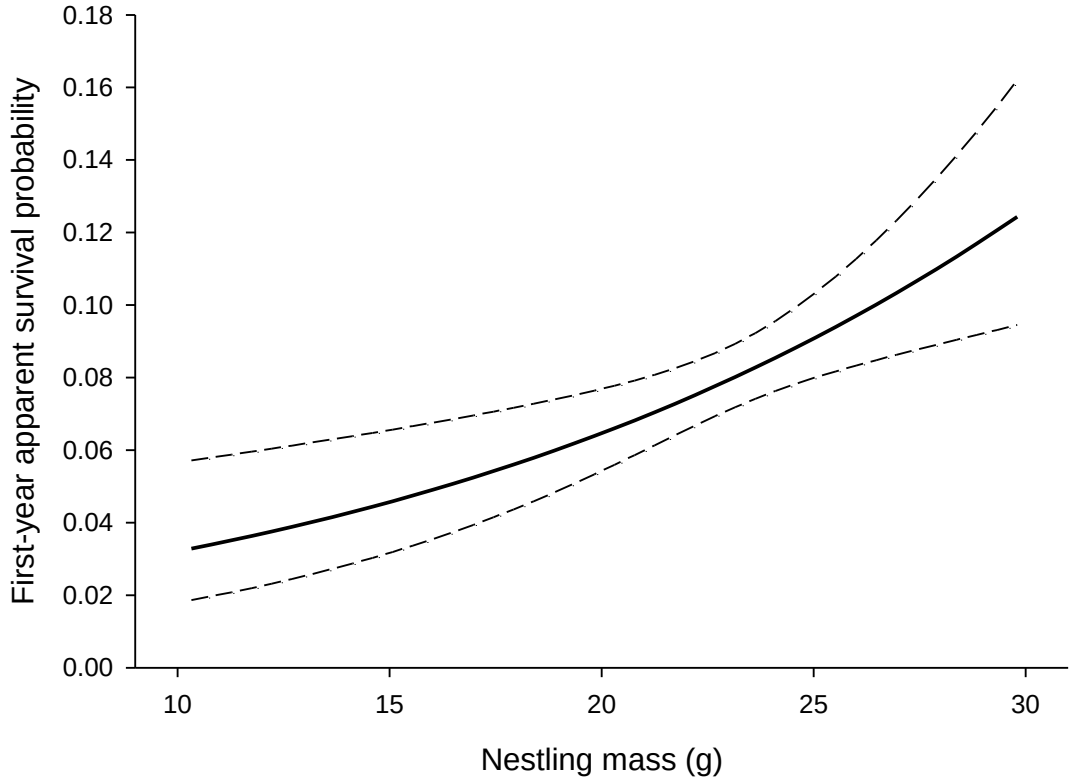


Fig. 4.1. First-year apparent survival probability (± 95% CI, dashed lines) of tree swallows (*Tachycineta bicolor*) at St. Denis National Research Area, Saskatchewan, 1991-2010, relative to body mass of nestlings at 12 days of age.

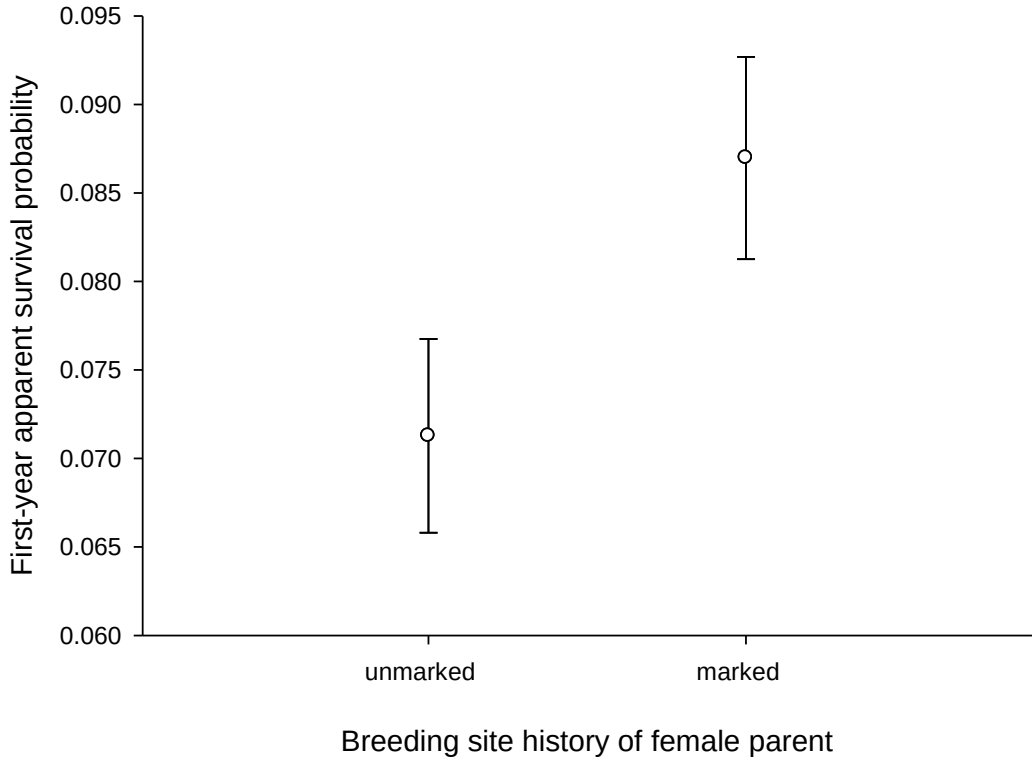


Fig. 4.2. First-year apparent survival probability (± 95% CI) of tree swallows (*Tachycineta bicolor*) at St. Denis National Research Area, Saskatchewan, 1991-2010, relative to breeding site experience of female parent. An unmarked female was one that had not been previously encountered in the colony, whereas a marked female had been encountered at the site during a previous year.

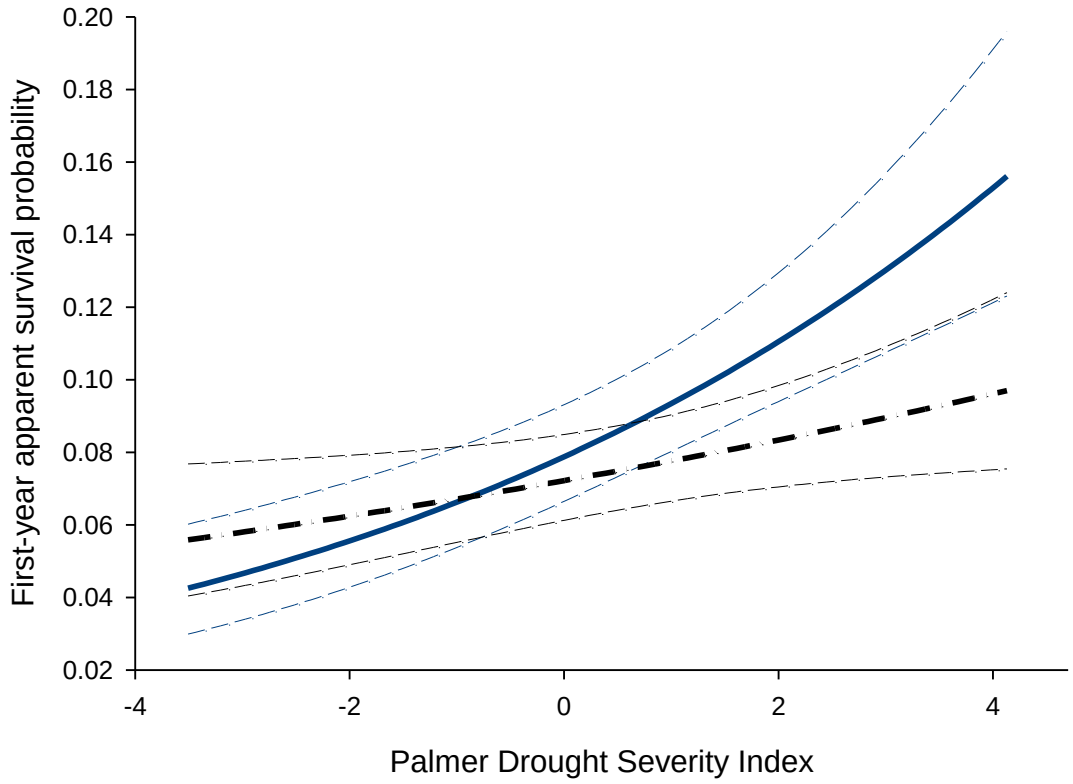


Fig. 4.3. First-year apparent survival probability (± 95% CI, dashed lines) of tree swallows (*Tachycineta bicolor*) at St. Denis National Research Area, Saskatchewan, 1991-2010, for nestlings of early initiating (< median; solid line, blue) and late initiating (≥ median; dash-dot line) parents relative to the mean Palmer Drought Severity Index from December-March of the winter prior to hatch. Negative index values signify drier conditions and positive values indicate wetter conditions.

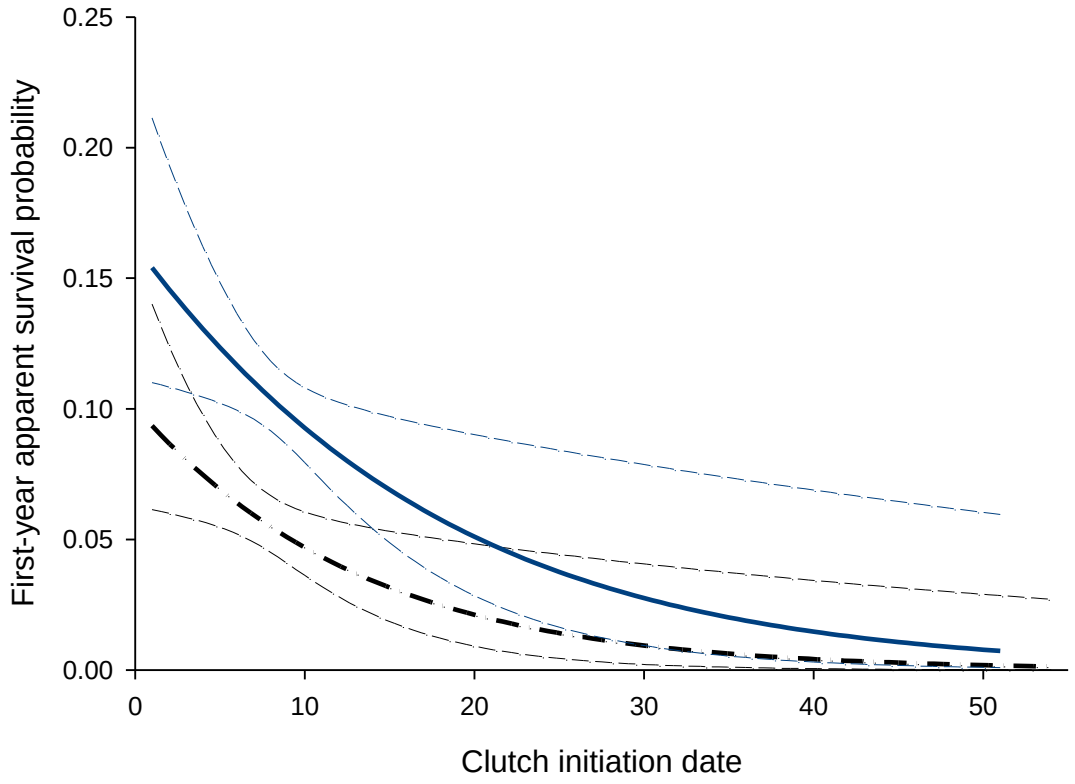


Fig. 4.4. First-year apparent survival probability (± 95% CI, dashed lines) of tree swallows (*Tachycineta bicolor*) at St. Denis National Research Area, Saskatchewan, 1991-2010, for individuals raised during years with positive (i.e., relatively wet conditions; solid line, blue) and negative (i.e., relatively dry conditions; dash-dot line) mean Palmer Drought Severity Index values from December-March of the winter prior to hatch relative to day of clutch initiation, where day 1 denotes first day of egg laying within each year.

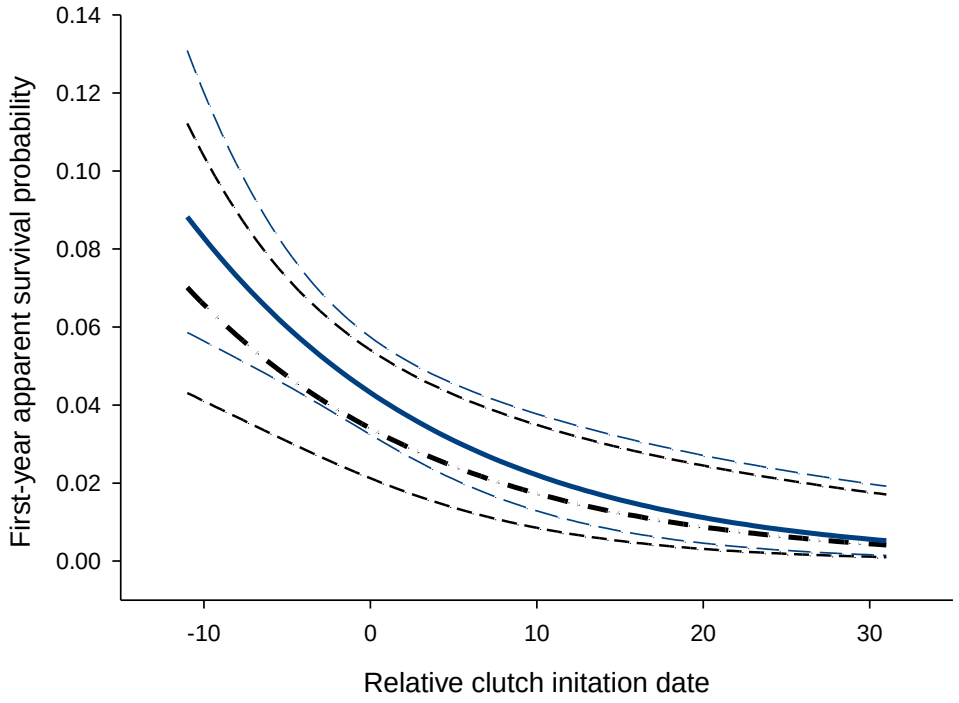


Fig. 4.5. First-year apparent survival probability (± 95% CI, dashed lines) of tree swallows (*Tachycineta bicolor*) at Prince George, British Columbia, 2001-2010, relative to the relative clutch initiation day, where 0 is the annual median clutch initiation day and values represent the number of days clutches were initiated earlier (negative) or later (positive) than the median date for clutch sizes of 4 (solid line, blue) and 7 (dash-dot line) eggs. Only two possible clutch sizes are shown for simplicity, smaller and larger clutches fall below or above each predicted line, respectively.

4.4 DISCUSSION

Despite suggestions that pre-breeding survival is the most important factor driving population dynamics of short-lived species (Emlen and Pikitch 1989, Noon and Sauer 1992), few studies have examined variables influencing first-year apparent survival of short-lived birds (but see Dybala et al. 2013a). To my knowledge, this is the first study to investigate factors influencing first-year apparent survival of an aerial insectivore. Furthermore, this research utilized mark-recapture data from two distinct areas of the tree swallow's breeding range. Individuals at these locations experience different environmental conditions (e.g., food abundance, Chapter 3) and exhibit differences in

demographic parameters, including apparent survival probabilities of adults (R. Clark et al. unpubl. data). Recent research also suggests that adults from these sites utilize different migratory routes and winter ranges (D. Bradley, University of Guelph, unpubl. data). My results indicate that effects of both parental and environmental quality were important predictors of first-year apparent survival of tree swallows, but findings were most congruent with the date hypothesis at both SDNRA and PG.

4.4.1 Effects of parental quality: breeding site familiarity of females

Breeding site experience of female parents was an important predictor of first-year apparent survival at SDNRA. With the exception of female recruits (and thus banded as nestlings) breeding at the site for the first time (< 15%) or females not captured during their first breeding attempt, this covariate reflects prior breeding experience at the site. Adult dispersal from breeding sites is low in tree swallows (Winkler et al. 2004, Hosner and Winkler 2007). However, only 10% of females new to the colony were 1-year-old and it seems unlikely that 1-year-old females of this short-lived species would delay breeding until ≥ 2 years old. High competition for nest sites may have resulted in 1-year-old females nesting elsewhere during their first breeding season (Winkler et al. 2005). Nonetheless, low adult dispersal rates suggest that previously unmarked females were younger than their banded counterparts. The age of first recapture of known-age females support the assumption that the majority of individuals without prior breeding site experience were likely 2-years-old at SDNRA, and thus the majority of those with prior breeding site experience were 3-years-old and older. Older females often attain higher reproductive success (Forslund and Pärt 1995, Robertson and Rendell 2001, Hatch and Westneat 2007) and produce more recruits (Blums et al. 2002). Yet past research has demonstrated that female age frequently acts indirectly on reproductive success and recruitment, as older females generally nest earlier and/or lay larger clutches. I did not observe a difference in clutch initiation date or clutch size between female parents with prior breeding site experience and those with none. I may have failed to observe these expected age-related patterns because 1-year-old females rarely bred at SDNRA and in

tree swallows, differences in clutch initiation date and clutch size are greatest between 1-year-old and all other females (Robertson and Rendell 2001). My results are unique in that I observed decreased apparent survival of offspring produced by younger females irrespective of clutch initiation date or clutch size and despite encountering few 1-year-old breeding females. Females with prior breeding site experience were heavier than inexperienced birds at SDNRA. Several studies have documented positive relationships between female mass or condition and reproductive success and pre-fledging offspring survival (Sanz 1995, Blomqvist et al. 1997, Gurney et al. 2012) and recruitment (Blums et al. 2002, Müller et al. 2005, Hegyi et al. 2011).

Prior breeding site experience of the female parent may influence first-year apparent survival independent of female age or mass. Prior breeding site experience has been linked to increased nesting success in western sandpipers (*Calidris mauri*; Johnson and Walters 2008), and familiarity with a breeding site increased fledging success of female piping plovers (*Charadrius melodus*), irrespective of female age (Saunders et al. 2012). Prior breeding site experience may improve a parent's local knowledge of the site resulting in the selection of better quality nesting sites or partners, or use of superior foraging sites (Saunders et al. 2012), resulting in higher quality offspring.

4.4.2 Effects of date: food abundance (Palmer Drought Severity Index, clutch size)

My results suggest that annual and/or seasonal variation in environmental quality were important predictors of first-year apparent survival at SDNRA and PG. Both date-related covariates suggest, although indirectly, that apparent survival was higher when food was more abundant.

Similar to Reid et al.'s (2008) report that first-year apparent survival of red-billed choughs (*Pyrrhocorax pyrrhocorax*) was greater for individuals that hatched during years when weather conditions favored invertebrate (food) abundance, the relationship between the Palmer Drought Severity Index and first-year apparent survival at SDNRA was likely driven by food availability. Tree swallows feed primarily on aerial insects of aquatic origin (Quinney and Ankney 1985, Blancher and McNicol 1991). Relatively wet periods

likely correspond with higher food abundance during the breeding season. Aerial insect abundance is greater during warmer springs with abundant wetlands (Fast 2007) and during breeding seasons following winters with greater precipitation (Blancher and Robertson 1987). Adult survival of tree swallows has been linked to moisture conditions, with increased survival in years following the presence of deeper wetlands at SDNRA (R. Clark, unpubl. data). Although greater food abundance is associated with greater body mass of nestling tree swallows (Quinney et al. 1986, Shutler et al. 2006), my results suggest that moisture conditions affected first-year apparent survival independently of pre-fledging body mass. Thus, results indicate that food abundance may have influenced an aspect of individual quality other than body mass. For example, greater per capita food abundance corresponded with increased immune function of nestling sand martins (*Riparia riparia*; Brzek and Konarzewski 2007) and barn swallows (*Hirundo rustica*; Saino et al. 1997). Stronger immune responses corresponded with greater recruitment probability, independent of body mass in fledgling pied flycatchers (*Ficedula hypolecuca*, Moreno et al. 2005) and house martins (*Delichon urbica*, Christe et al. 2001). Examination of the interaction between clutch initiation date and the Palmer Drought Index revealed that first-year apparent survival of tree swallows decreased with later hatching dates regardless of whether individuals were raised during relatively wet or dry conditions at SDNRA. This may indicate that either: (i) food was seasonally limiting during both wet and dry years, (ii) some other factor associated with environmental quality declined during both wet and dry years, and/or (iii) some unmeasured attribute of parental quality declined seasonally.

Although the Palmer Severity Drought Index was an important predictor of apparent survival at SDNRA, it was not at PG. The range of PSDI values indicated that this covariate was less variable at PG than SDNRA during the years of study and always fell in the average to wet range. At PG, I observed the opposite than expected trend with respect to clutch size, despite the positive relationships between clutch size and female mass, age and breeding site experience. I predicted that high-quality females would lay larger clutches (Winkler and Allen 1996, Pettifor et al. 2001, Schoech et al. 2008), and yet first-year apparent survival was negatively related to clutch size. Clutch size and

brood size throughout the nestling period were positively correlated at PG. Individuals from larger broods may have experienced lower first-year apparent survival probabilities as a result of receiving less food. Indeed, brood size manipulation studies in tree swallows have demonstrated that parents alter their feeding rates, but are not able to fully compensate for increased brood sizes (Shutler et al. 2006, Bortolotti et al. 2011). More nestlings from larger clutches died prior to fledging than from smaller clutches (V. Harriman et al. unpubl. data). Although clutch size was moderately correlated with RCID, my results suggest that the effect of clutch size on apparent survival was independent of clutch initiation date. At PG, there appeared to be a paradox: high quality individuals laid larger clutches but larger clutches produced offspring with lower survival probabilities. Why did better quality individuals at PG continue to lay larger clutches? Better quality individuals may lay larger clutches at little cost to themselves and larger clutches may produce more recruits under ideal conditions. It is likely that reproductive investment decisions by tree swallows are based largely on food abundance during egg laying rather than on food abundance during the nestling period (Dunn et al. 2011). A lack of correlation between aerial insect abundance during egg laying and the nestling period may have contributed to this pattern. Furthermore, tree swallows display remarkable consistency in clutch size relative to clutch initiation date across North America (Winkler et al. 2002) and thus the relationship between clutch size and clutch initiation date may be a relatively inflexible life-history trait in tree swallows. It is also important to note that despite higher nestling mortality rates in larger clutches, individuals that laid larger clutches produced more fledglings than those that laid smaller clutches (VBH et al. unpubl. data). Although apparent survival of individuals from larger clutches was lower than that of individuals from smaller clutches, the actual number of recruits from each clutch may not have differed. Assuming that adult female survival probability or future reproductive success are unrelated to current clutch or brood sizes, there may be no fitness costs of producing larger clutches.

4.4.3 Effects of nestling mass & timing of breeding

Perhaps unsurprisingly, timing of egg laying (clutch initiation date at SDNRA and relative clutch initiation date at PG) were important predictors of first-year apparent survival at both sites. Higher apparent survival of early-hatched individuals was likely attributed to factors associated with both the quality and date hypotheses. Although I investigated the effect of covariates consistent with either the quality or date hypothesis, the retention of covariates of timing of egg laying in top-ranked models indicates that some unmeasured attribute(s) of parental and/or environmental quality contributed to first-year apparent survival in tree swallows.

At SDNRA, timing of clutch initiation influenced apparent survival independently of prior breeding site experience of female parents and nestling body mass, but there was an interaction between clutch initiation date and the Palmer Drought Severity Index. Interestingly, early-initiating parents produced offspring that were more likely to survive than late-initiating parents during wet years when compared to dry years. A central prediction of the quality hypothesis is that high-quality individuals breed earlier than low quality individuals (e.g., Ardia 2005a, O'Brien and Dawson 2013), and my results may reflect the superior ability of early-initiating parents to utilize available resources such as food. Although I am unaware of studies demonstrating a disproportional benefit of better environmental quality on early breeders, supplemental feeding prior to and during egg laying results in increased clutch sizes, primarily via the advancement of clutch initiation date (Schoech et al. 2008). Indeed, data reveal that clutch sizes were larger in wetter years, but that this relationship was stronger for early-initiating than late-initiating parents (V. Harriman unpubl. data). Because one limitation of early breeding in tree swallows is food abundance during egg production (Nooker et al. 2005), the reproductive investment of relatively early-breeding individuals may be more constrained by food available during egg production than late-breeding individuals. Wet conditions during December – March prior to the breeding period may have resulted in disproportionately greater food abundance early in the breeding season relative to that later in the breeding season.

Larger and heavier offspring have greater recruitment rates in many avian species (Perrins 1965, Tinbergen and Boerlijst 1990, Brinkhof et al. 1997, Both et al. 1999,

Medeiros and Freed 2009) including tree swallows (Shutler et al. 2006). Body mass of nestlings close to fledging can be influenced by multiple factors in any given year, including food abundance and weather conditions (Dawson and Bortolotti 2000, Shutler et al. 2006, Dawson 2008), and high-quality females appear to produce heavier nestlings (Brinkhof et al. 1997, Blums et al. 2002, Wardrop and Ydenberg 2003, Nooker et al. 2005). The inclusion of the additive effect of clutch initiation date in the top-ranked model at SDNRA suggests that body mass of nestlings influenced apparent survival regardless of when during the season they were raised. Interestingly, body mass of nestlings was not a good predictor of apparent survival at PG. An additional additive effect of body mass of nestlings was possibly not supported because this factor was accounted for by the inclusion of relative clutch initiation and clutch size. After accounting for random effects of nest id and year, nestlings were progressively lighter with hatching date (VBH et al. unpubl. data) and from larger clutches.

4.4.4 Conclusion

First-year apparent survival of tree swallows is related to several interacting factors. High-quality parents may enhance the innate quality of offspring (Cichoń et al. 2006, Hegyi et al. 2011), and/or they may raise better quality offspring (Brinkhof et al. 1997, Daunt et al. 1999, Hipfner and Gaston 2002). Overwhelmingly, studies investigating parental and environmental quality effects on local recruitment of songbirds have been consistent with predictions of the date hypothesis (review in Verhulst and Nilsson 2008, Öberg et al. 2013). The only direct parental quality index retained in a top-ranked model at SDNRA - prior breeding site experience of female parents - did not suggest that this attribute of parental quality was different for early and late-initiating parents. At PG, clutch sizes were smaller later in the season and clutch size was positively correlated with multiple indices of female quality. And yet the relationship between clutch size and first-year apparent survival was opposite than expected. My results suggest that, although the contribution of parental quality to lower fitness of late

breeders is uncertain, first-year apparent survival of tree swallows cannot be attributed to factors of date alone.

Young birds must learn critical skills after fledging and prior to the onset of migration (Weathers and Sullivan 1989, Wheelwright and Templeton 2003, Yoda et al. 2004). Mortality is often high during the early post-fledging period and timing of fledging and condition of fledglings are important predictors of survival during this stage (Naef-Daenzer et al. 2001, Dybala et al. 2013b). Although apparent survival of adult migratory birds is often linked to climatic conditions during migration and on the wintering grounds (Sillett et al. 2000, Mazerolle et al. 2005, Franke et al. 2011, LaManna et al. 2012, RGC unpubl. data) the preponderance for mortality soon after fledging may be why I did not observe an effect of non-breeding season climate on first-year apparent survival (but see Mihoub et al. 2010).

There has been particular interest in identifying when and which attributes associated with date influence fitness-related traits of organisms, particularly in the context of determining potential consequences of climate change (Lyon et al. 2008, Visser 2008). Declining food abundance during the breeding season is often proposed as the primary mechanism for declining environmental quality for birds (Perrins 1970, Siikamäki 1998, Verboven et al. 2001). And although some studies have documented seasonal declines in aerial insects (Grüebler and Naef-Daenzer 2008, Chapter 3), a long-term, multi-site study by Dunn et al. (2011) noted that insect abundance increased during the nestling period in half of the site-years and was otherwise variable. Although some of my results suggest that seasonal declines in food abundance during the breeding season may play a role in explaining lower fitness of late breeders, direct measures of the effects of seasonally varying food availability on apparent survival has yet to be addressed.

At SDNRA, the relationship between apparent survival and a direct measure of environmental quality (PSDI) indicated that annual variations in moisture had important consequences for first-year apparent survival of tree swallows. Although timing of breeding is an important factor to consider in the context of effects of changing climatic conditions (Both et al. 2006, Lyon et al. 2008), temporal variation in environmental quality on the breeding grounds may provide important insights into drivers of population

trends, particularly for aerial insectivores. Climate predictions for drier pre-breeding conditions in many parts of North America, but particularly in southwestern North America (IPCC 2013), may have significant negative impacts on aerial insectivore populations. Conversely, predictions for wetter pre-breeding conditions in northern North America (IPCC 2013) may be advantageous for many breeding populations. My results highlight the importance of considering regional precipitation trends when making projections of effects of climate change on demography of aerial insectivores.

CHAPTER 5: SYNTHESIS

5.1 SEASONAL VARIATION IN COMPONENTS OF AVIAN FITNESS: PATTERNS AND MECHANISMS

Unresolved questions about drivers of declines in fitness with later breeding dates abound in the avian literature since the seminal paper by Perrins (1970). Recent efforts have been made to experimentally address predictions associated with the date and quality hypotheses, and the approach has often been to distinguish whether factors of date *or* quality were acting on fitness-related parameters during the year(s) of experimental study. These hypotheses are not mutually exclusive and there are *a priori* reasons to expect both parental and environmental quality to contribute to temporal patterns in fitness (see review in Verhulst and Nilsson 2008). Furthermore, the importance of quality or date could vary annually, depending on environmental conditions in any given year (e.g., timing of weather events; Dawson 2008). Thus, assessment of the relative influence of parental or environmental quality on fitness-related variables provides a more realistic approach to answering questions related to effects of timing of breeding on fitness (e.g., Verhulst et al. 1995). Despite this, few studies have simultaneously considered effects of parental and environmental quality on fitness-related traits in the context of declines in fitness with later breeding dates (but see Gurney et al. 2012). Furthermore, because there is particular interest in making predictions about consequences of environmental change on avian fitness, identifying the mechanisms underlying a seasonally deteriorating environment is imperative.

In Chapters 2 and 3 I used experiments and a statistical modelling framework to test two mechanisms proposed to contribute to a seasonal decline in environmental quality, an increase in nest ectoparasite abundance and a decrease in food abundance with later breeding dates. Although investigations into effects of parasite and food abundance are prevalent in the literature, direct tests investigating the seasonal variation of these effects are not. In a short-term experimental framework, one ideally controls for parental quality by altering the timing of breeding of some individuals. Although I did not experimentally alter hatching date when testing whether a seasonal increase in nest parasites contributed to a decline in nestling quality with later hatching dates, predicted indices of environmental quality (parasite and food abundance) suggested that environmental quality increased with later hatching dates at PG, thus providing the opportunity to further tease apart effects associated with each hypothesis.

Because numbers of blow flies decreased, rather than increased, with later hatching dates during this study, and flea abundance did not vary throughout the breeding season, it does not appear as though a seasonal decline in reproductive success was related to increasing nest parasite loads. Although decreasing blow fly numbers within a breeding season has been documented in other study systems (Hori and Iwasa 1988, Johnson et al. 1991), a seasonal increase (Pinkowski 1977, Wittmann and Beason 1992, Merino and Potti 1995) or no seasonal change in blow fly abundance (Bortolotti 1985, Hurtrez-Boussès et al. 1998, Dawson et al. 2005a, O'Brien and Dawson 2008) has been more commonly observed. Furthermore, CMI response appeared to increase with food abundance (i.e., greater response by late-hatched individuals) at PG, indicating that a reduction in the ability of nestlings to mount an immune response with later hatching dates was unlikely. Despite these findings, at PG where blow fly loads were greater, experimental reductions of parasites provided insights into putative trade-offs, and suggested that early- and late-hatched nestlings allocated energy differently in response to parasites. There was a disproportionate benefit of parasite removal on length of primary feather for early-hatched nestlings, indicating greater energetic constraints early in the breeding season. Furthermore, late-hatched nestlings from parasite-removal nests had

longer head-bill length than their control counterparts and developed head-bills of similar length to those of early-hatched nestlings at PG.

Despite these findings, and in accordance with previous studies ((size: Merino and Potti 1998; Thomas and Shutler 2001; Shutler et al. 2004) (growth: Roby et al. 1992; Wittmann and Beason 1992) (immunity: Saino et al. 1998; Tschirren et al. 2007; Brommer et al. 2011)) there were few detectable effects of ectoparasites on nestling size, growth and immunity (Table 5.1). In fact, negative effects of parasites were only apparent at PG when food (i.e., insect) biomass was considered. Parasite loads and food abundance are rarely measured simultaneously in the same study (but see Thomas et al. 2007), but it has been suggested that negative effects of parasites may only be apparent during periods of low food abundance (Johnson and Albrecht 1993). My results concur with this idea. Ultimately, results of this experiment suggested that although parasite-mediated trade-offs consistent with the date hypothesis were present at PG, nestling survival to fledging and local recruitment were consistent with the parental quality hypothesis. To my knowledge, parasitism as a mechanism of deteriorating environmental quality had not been tested prior to this study.

Since the seminal studies by Lack (1954) and Perrins (1970), it has been supposed that birds start breeding so the nestling period corresponds with peak food availability. The relationship between clutch initiation date and reproductive success frequently has been correlated with seasonal declines in food abundance (Norris 1993; Dawson 2008; Öberg et al. 2013). A widely-held belief is that seasonally declining food availability is an important factor mediating seasonal trends in fitness in avian ecology; to my knowledge, there has only been one published, experimental investigation of food abundance on declining reproductive success within a first breeding attempt while controlling for parental quality (Siikamäki 1998).

I experimentally tested whether declines in food abundance with later hatching dates contributed to seasonally deteriorating environmental conditions while controlling for parental quality (Chapter 3). In addition to examining the effect of manipulations, I also considered indices of environmental (e.g., insect biomass) and parental (e.g., body condition) quality on nestling quality, fledging success and return rates. Reduced

reproductive success of late-breeding individuals in this study was casually related to a seasonal decline in environmental quality (Table 5.1). Declining insect biomass and brood size enlargement resulted in nestlings that were lighter, in poorer body condition, had shorter head-bill lengths, shorter and slower growing ninth primary feathers and were less likely to survive to fledge. Results imply costs of seasonally diminishing food supply on fecundity-independent fitness of late-breeding individuals. There was little indication that early-nesting individuals raised better quality nestlings than late-nesters, although nestlings were in better body condition and were heavier at 16-days-old when raised by females in better body condition. While these findings suggest that female quality is an important predictor of some indices of nestling quality, body condition of females did not decrease with later breeding dates and thus results were not consistent with predictions of the parental quality hypothesis. Although high quality parents may nest earlier in many study systems (e.g., Blums et al. 2002, Ardia 2005b, Clark et al. 2014), the fitness benefits of early-breeding may be independent of the observed decline in reproductive success with later hatching dates and may be manifested via benefits of residual reproductive value, such as the likelihood of double-brooding or increased adult survival (Blums et al. 2005, O'Brien and Dawson 2013).

Investigations into potential mechanisms driving seasonal deterioration in the environment and how these contribute to decreased reproductive success with later nesting dates suggested that nest parasites may play a role influencing some aspects of nestling size, but food abundance had the greatest effect on fitness-related traits in this aerial insectivore. Results from long-term data (Chapter 4) corroborated findings of short-term manipulations (Table 5.1).

Despite suggestions that pre-breeding survival is the most important factor driving population dynamics of short-lived species (Emlen and Pikitch 1989, Noon and Sauer 1992), few studies have examined factors influencing first-year apparent survival of short-lived birds (but see Dybala et al. 2013a). In Chapter 4, I examined seasonal variation in first-year apparent survival of tree swallows (*Tachycineta bicolor*) at two distinct breeding locations using mark-recapture data (1991-2010 at SDNRA and 2001-2010 at PG) to investigate the relative influence of large-, small- and individual-scale

factors associated with the quality and date hypotheses. To my knowledge, this is the first study to investigate factors influencing first-year apparent survival of an aerial insectivore. Results indicated that effects of both parental and environmental (local-scale) quality were important predictors of first-year apparent survival of tree swallows, but findings were more consistent with the date hypothesis at both SDNRA and PG.

At SDNRA, the top model explaining first-year apparent survival of tree swallows included nestling mass, the female parent's breeding site experience and an interaction between the Palmer Drought Severity Index (PDSI) and clutch initiation date. First-year apparent survival of tree swallows at SDNRA was higher for heavier nestlings and those produced by females with prior breeding site experience. Apparent survival declined with later clutch initiation dates and overall apparent survival was higher during relatively wet years (i.e., years with positive PSDI values). At PG, first-year apparent survival was higher for individuals produced by parents with relatively early clutch initiation dates but lower for fledglings from larger clutches (an opposite than expected trend). Results suggest that annual and/or seasonal variation in environmental quality were important predictors of first-year apparent survival at SDNRA and PG. Both date-related covariates (PDSI at SDNRA, clutch size at PG) suggest, although indirectly, that apparent survival was higher when food was more abundant.

Overwhelmingly, studies investigating parental and environmental quality effects on local recruitment (i.e., number of individuals returning rather than apparent survival probabilities) of songbirds have been consistent with predictions of the date hypothesis (review in Verhulst and Nilsson 2008, Öberg et al. 2013). Indeed, the only direct parental quality index retained in a top-ranked model at SDNRA, prior breeding site experience of female parents, did not differ between early and late-initiating parents. At PG, clutch sizes were smaller later in the season and clutch size was positively correlated with multiple indices of female quality. And yet the relationship between clutch size and first-year apparent survival was opposite than expected. Environmental factors appeared to drive *seasonal variation* in first-year apparent survival, and yet first-year apparent survival of tree swallows was related to several interacting factors. Results from Chapter 4 suggest that the contribution of parental quality to lower fitness of late breeders is

uncertain, yet first-year apparent survival of tree swallows cannot be attributed to factors of date alone.

Collectively, my research suggests that parental and environmental quality influence seasonal variation in fitness-related traits of tree swallows. However, the strongest evidence indicates that environmental quality, and in particular food abundance, had the greatest effect on seasonal variation in nestling quality, reproductive success and first-year apparent survival in tree swallows. It is important to note that individual and environmental quality are challenging to measure with certainty. The tree swallow was a useful avian model to test the importance of food on seasonal variation in environmental quality because they feed almost exclusively on flying insects. And although sampling aerial insects is difficult, obtaining a useful index of seasonal variation in food abundance is easier for swallows than for species with more diverse diets. Comparatively, indexing individual quality is much more challenging. Two of the best measures of individual quality are individual survival and survival of offspring, and yet determining whether there is a short-term, easily measured and reliable index of individual quality that can aid us in predicting these components of fitness is immensely challenging. Regardless, I believe that my work provides important new insights into drivers of seasonally varying fitness in animals. In light of the challenges of indexing parental quality, the experiment in Chapter 3 provided a strong, direct test of the quality and date hypotheses.

Although timing studies are numerous, there are still many questions left unanswered. Avian timing studies suffer from a taxonomic bias. The majority of timing studies have focused on seabirds and insectivorous, hole-nesting passerines. Future research should aim to provide insight into whether current findings are broadly relevant. A predominant question arising in the timing of breeding literature is why late-breeding individuals fail to breed earlier if early-breeding is advantageous. Research to date has been limited to short-term fitness costs of timing of breeding, focusing on reproductive success of individuals within a year. The investigation of longer-term fitness consequences of timing of breeding for individuals using mark-recapture methods may provide an exciting research avenue.

Table 5.1. Timing of breeding and nestling quality and first-year apparent survival in tree swallows (*Tachycineta bicolor*): summary of hypotheses tested and key findings.

Hypothesis	Predictions	Key findings
Chapter 2: Ectoparasite abundance as mediator of deteriorating environmental quality		
Date: ectoparasites	• Ectoparasite loads increase with later hatching dates	• Opposite to predicted, numbers of blow flies decreased seasonally, no seasonal trend in flea abundance
	• Removal of ectoparasites (treated) result in better quality nestlings (larger, grow faster, larger PHA response, lower levels of $CORT_F$, higher recruitment rates) and would be disproportionately beneficial for late-hatched nestlings	• Partially consistent with predictions • PG: Longer head-bill lengths of treated relative to un-treated nestlings for late-hatched individuals only; thus beneficial for late-hatched nestlings only • PG: Longer ninth primary feathers of treated early-hatched nestlings relative to their treated late-hatched counterparts; thus beneficial for early-hatched nestlings only • SD: $CORT_f$ was lower in treated nestlings
Quality	• Early-initiating parents would raise nestlings of better quality regardless of ectoparasite treatment and anti-parasite treatment would not be disproportionately beneficial for late-hatched nestlings; this prediction could only be indirectly tested due to the apparent seasonal improvement in environmental quality at PG	• Partially consistent with predictions • PG: Early-hatched nestlings had similar length of primary feathers to their late-hatching counterparts despite poorer environmental quality • PG: Early-hatched nestlings had longer length of head-bill than late-hatched nestlings in control nests despite poorer environmental quality

		• PG: Early-nesting parents were more likely to produce a brood in which all nestlings survived to fledging and at least one nestling recruited locally despite poorer environmental quality
Chapter 3: Food abundance as mediator of deteriorating environmental quality		
Date: food	• Insect biomass decreases with later hatching dates	• Consistent with prediction
	• Nestlings in enlarged broods (i.e., with reduced food per capita) would be of lower quality and less likely to survive to fledging or return in subsequent years than their control counterparts and this relationship would be more pronounced later in the season regardless of when parents initiated nests	• Consistent with predictions • Declining insect biomass and brood size enlargement resulted in nestlings that were lighter, in poorer body condition, had shorter head-bills, shorter and slower growing ninth primary feathers and less likely to survive to fledge
Quality	• Indices of parental quality should be good predictors of nestling quality and indicate that parental quality decreases with later hatching dates	• Not consistent with prediction
	• Delayed parents should produce better quality nestlings than non-delayed parents with the same hatching date	• Not consistent with prediction
Chapter 4: Effects of parental and environmental quality on first-year apparent survival		
Date	• Climate: First-year apparent survival should be highest during El Niño fall migrations	• Not consistent with prediction

	• Local Habitat: Greater apparent survival during years when it is wetter on breeding grounds (i.e., more food)	• SD: consistent with prediction • PG: not consistent with prediction
Quality	• Older parents should be better quality; therefore, first-year apparent survival should be greater for individuals raised by older females	• Not consistent with prediction
	• Higher quality parents should have greater body mass; therefore, first-year apparent survival should be greater for individuals with heavier female parents	• Not consistent with prediction
	• Parents with prior breeding site experience should produce offspring with greater apparent survival probabilities	• SD: consistent with prediction • PG: not consistent with prediction
	• Higher quality females should lay larger clutches; therefore, first-year apparent survival should be greater for individuals originating from larger clutches	• SD: not consistent with prediction • PG: Opposite to predicted; first-year apparent survival lower for individuals from larger clutches; results more consistent with predictions of date hypothesis

5.2 IMPLICATIONS FOR CONSERVATION OF AERIAL INSECTIVORES

Identifying when and which attributes associated with date influence fitness-related traits of organisms is essential to predicting potential consequences of climate change (Lyon et al. 2008, Visser 2008). Aerial insectivores are experiencing population declines throughout much of North America (Nebel et al. 2010, Shutler et al. 2012). The causes of these declines are unknown and efforts are currently being made to evaluate possible explanations for these trends. A mismatch between timing of breeding and food availability, and declines in habitat quality and food abundance, have been proposed as possible mechanisms (Nebel et al. 2010). Although evidence suggests that there is no mismatch between timing of breeding and food availability for tree swallows (Dunn et al. 2011), a mismatch between food availability and the timing of other energy-costly stages during the annual cycle (e.g., fall migration) is plausible (D.W. Winkler personal communication).

This thesis focuses on factors influencing nestling quality and fledgling survival (i.e., recruitment and apparent survival probabilities) and thus provides some insight into possible factors limiting these life-history stages in tree swallows. Importantly, it has been suggested that pre-breeding survival is the most important factor driving population dynamics of short-lived species (Emlen and Pikitch 1989, Noon and Sauer 1992). Furthermore, tree swallows provide a good model because although they are declining in some areas of their range (Shutler et al. 2012), their populations are sufficiently large to facilitate intensive monitoring and manipulations, and hence provide opportunities to conduct robust tests of competing hypotheses. Because the greatest commonality among aerial insectivore species is that they feed on aerial insects, one of the primary hypotheses of interest is that a change in food abundance is contributing to population declines.

My results suggest that seasonal declines in food abundance during the breeding season may play a pivotal role in explaining lower fitness among late breeders. In particular, my study, for which I concurrently accounted for parental quality and manipulated food availability per capita, while simultaneously considering indices of parental and environmental quality on two study sites over two breeding seasons,

provides evidence for the importance of food resources in mediating seasonal declines in avian offspring quality and survival (Chapter 3). Yet a long-term, multi-site study by Dunn et al. (2011) noted that insect abundance increased during the nestling period of tree swallows in half of the site-years and was otherwise variable. As such, temporal variation in environmental quality on the breeding grounds may also provide important insights into drivers of population trends. Indeed, there is strong annual variation in adult survival across the breeding range of tree swallows (RGC et al. unpubl. data). At SDNRA, the relationship between apparent survival and a direct measure of environmental quality (PSDI) indicated that annual variation in moisture had important consequences for first-year apparent survival of tree swallows (Chapter 4). Aerial insect abundance is greater during relatively wet conditions (Blancher and Robertson 1987, Fast 2007).

Local- and regional-scale changes in the environment may have important implications for populations of aerial insectivores. Throughout much of the range of many aerial insectivores, land use practices have resulted in extensive habitat modification and the drastic reduction in the number of wetlands (Dahl 1990, Prairie Habitat Joint Venture 2008) for which many aquatic insects rely on to breed. Furthermore, climate predictions for drier pre-breeding conditions in many parts of North America, but particularly in southwestern North America (IPCC 2013), may have significant negative impacts on aerial insectivore populations. Conversely, predictions for wetter pre-breeding conditions in northern North America (IPCC 2013) may be advantageous for many breeding populations. These results highlight the importance of considering local land use practices and regional precipitation trends when making projections of changes in demography of aerial insectivores.

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APPENDIX 1: SUMMARY STATISTICS OF BOX USE AND FLEDGING AND RECRUITMENT

Table A1.1. Total number of tree swallows *(Tachycineta bicolor*) that fledged and recruited by year, using *unrestricted* datasets (see Methods for details) at the St. Denis National Research Area (SDNRA) and near Prince George, British Columbia. The number of recruits includes banded nestlings recaptured until 2012. Also reported are the total number of boxes on each site and the proportion of boxes occupied (pct. occupancy) by year.

Site	Year	No. boxes	Pct. occupancy	No. fledglings	No. recruits
SD	1991	75	0.92	22	0
	1992	100	0.91	289	14
	1993	115	0.91	30	1
	1994	115	0.85	30	3
	1995	115	0.91	352	23
	1996	127	0.93	438	26
	1997	115	0.98	608	46
	1998	124	1.00	551	40
	1999	124	0.96	323	8
	2000	131	0.97	619	26
	2001	150	0.94	644	13
	2002	145	0.81	420	11
	2003	159	0.88	596	36
	2004	160	0.82	331	13
	2005	160	0.91	700	41
	2006	160	0.99	874	54
	2007	185	0.99	881	56
	2008	209	0.97	901	56
	2009	234	0.94	854	43
	2010	255	0.99	917	20
PG	2001	196	0.27	70	2
	2002	337	0.26	159	6
	2003	322	0.33	179	10
	2004	293	0.47	434	16
	2005	273	0.49	409	14
	2006	263	0.54	532	25
	2007	243	0.59	411	22
	2008	286	0.52	415	13
	2009	278	0.54	433	16
	2010	271	0.58	437	13

APPENDIX 2: PREDICTED RELATIONSHIPS BETWEEN INDICES OF PARENTAL AND ENVIRONMENTAL QUALITY WITH FIRST-YEAR APPARENT SURVIVAL

Table A2.1. Associated hypothesis and predicted relationship with first-year apparent survival of tree swallows (*Tachycineta bicolor*) at the St. Denis National Research Area, Saskatchewan (SDNRA), 1991-2010, and near Prince George, British Columbia (PG), 2001-2010 of covariates considered in the final models (a) and additional climate factors considered in initial models (b).

	Category	Variable	Variable code	Hypothesis	Predicted relationship with survival	Rational	Source
(a)							
	Climate	ENSO; Mean Southern Oscillation Index (SOI) during fall migration (August - September; PG only)	SOI_fall	Date	Negative (highest in El Niño years)	Warmer temperatures reduce energy expenditure during fall migration (El Niño years)	Stokke et al. 2005
		ENSO; Mean bivariate ENSO Timeseries (BEST) during fall migration (August - September; SDNRA only)	BEST_fall		Positive (highest in El Niño years)		
	Local habitat	Mean Palmer Drought Severity Index December - March preceding hatch	PSDI	Date	Positive	Greater insect abundance during natal summer in wetter years	Blancher and Robertson 1989, Holmgren et al. 2001, Dybala et al. 2013
	Local habitat	May depth of semi-permanent wetland (SDNRA only)	pond	Date	Positive	Greater insect abundance during natal summer in wetter years	Blancher and Robertson 1989, RGC unpublished data
	Individual	Minimum age of female parent	fem_age	Quality	Positive	Older females are better quality parents	Forslund and Pärt 1995, Robertson and Rendell 2001, Blums et al. 2002
	Individual	Mass of female parent	fem_mass	Quality	Positive	Better quality parents are heavier	Blums et al. 2002, Müller et al. 2005, Hegyi et al. 2011

	Individual	Breeding site history of female parent	fem_recap	Quality	Positive	Females with prior breeding site experience are better quality parents	Saunders et al. 2012
	Individual	Clutch size	clutchsz	Quality	Positive	Better quality females lay larger clutches	Winkler and Allen 1996, Pettifor et al. 2001, Schoech et al. 2008
	Individual	Nestling mass (day 12)	mass	Date/Quality	Positive	Heavier nestlings are more likely to survive than light nestlings	Brinkhof et al. 1997, Shutler et al. 2006
	Individual	Standardized clutch initiation date (day 1 = first egg laid within year and site)	CID	Date/Quality	Negative	Early-hatched nestlings are more likely to survive than late-hatched nestlings	Blums et al. 2002, Shutler et al. 2006
		Relative clutch initiation date (day 0 = median clutch initiation within year and site)	RCID				

(b)

	Climate	North Atlantic Oscillation Index	NAO_winter	Date	Positive	Food abundance is higher and energy expenditure is lower during warmer and wetter winter conditions	Balbontin et al. 2009
	Climate	SOI or BEST on breeding grounds	ENSO_summer	Date	Highest in El Niño years	Warmer temperatures during the breeding season will result in fledglings in better condition	McCarty and Winkler 1999, Dawson 2008
	Climate	SOI or BEST during spring migration	ENSO_spring	Date	Highest in El Niño years	Food abundance is higher during wetter conditions (but effects of SOI generally weak in spring)	LaManna et al. 2012

Climate	SDNRA; SOI or BEST on wintering grounds	ENSO_winter	Date	Lowest in El Niño years	Food abundance is higher during wetter conditions in Mexico along the Gulf of Mexico and in Florida (La Niña years)	Sillett et al. 2000, Mazerolle et al. 2005, Holmgren et al. 2001
Climate	PG; SOI or BEST on wintering grounds	ENSO_winter	Date	Highest in El Niño years	Food abundance is higher during wetter conditions in California and northwestern Mexico (El Niño years)	LaManna et al. 2012, Nott et al. 2002;
Climate	Pacific Decadal Oscillation on wintering grounds	PDO_winter	Date	Positive	Food abundance is higher during wetter conditions in southern United States and Mexico	Ballard et al. 2003, Vanderbosch 2003, LaManna et al. 2012, McClure et al. 2012
Climate	Pacific-North American Teleconnection on wintering ground	PNA_winter	Date	Positive	Food abundance is higher during wetter conditions in southern United States and Mexico	Møller et al. 2010

APPENDIX 3: FIRST-YEAR APPARENT SURVIVAL MODEL SELECTION RESULTS

Model selection results for models incorporating covariate effects on first-year apparent survival of tree swallows (*Tachycineta bicolor*) at the St. Denis National Research Area, Saskatchewan (SDNRA), 1991-2010, and near Prince George, British Columbia (PG), 2001-2010 for *unrestricted* (Table A3.1), *restricted* (Table A3.2) and *highly restricted* (Table A3.3) data sets (see Methods) and parameter estimates (on logit-link scale) and associated standard errors (SE). Models with $\Delta AIC_c < 4$ (SDNRA) or < 2 (PG) are reported for brevity.

Table A3.1. *Unrestricted* data set.

Site	n	No. recruits	Model structure[a]	K[b]	-2logL[c]	AIC_c[d]	ΔAIC_c[e]	ω_i[f]	Parameter[g]	Estimate	SE
SDNRA	10381	530	PDSI * CID + CID_nonlin + mass + fem_recap	11	7076.873	7098.896	0.000	0.773	ϕ: β_0	-3.913	0.537
									ϕ: β_{PDSI}	0.219	0.045
									ϕ: β_{CID}	-0.069	0.020
									ϕ: $\beta_{PDS*CID}$	-0.011	0.005
									ϕ: $\beta_{CID\ nonlin}$	0.001	0.001
									ϕ: β_{mass}	0.073	0.022
									ϕ: $\beta_{fem\ recap}$	0.216	0.095
									p: β_1	-1.259	0.098
									p: β_2	0.377	0.109
			PDSI + CID + CID_nonlin + mass + fem_recap	10	7082.875	7102.895	3.998	0.105	ϕ: β_0	-3.867	0.536
									ϕ: β_{PDSI}	0.129	0.025
									ϕ: β_{CID}	-0.074	0.020
									ϕ: β_{CID_nonlin}	0.001	0.001
									ϕ: β_{mass}	0.074	0.022
									ϕ: $\beta_{fem\ recap}$	0.219	0.095
									p: β_1	-1.257	0.098
									p: β_2	0.380	0.109
PG	3480	137	clutchsz + RCID	7	1697.278	1711.309	0.000	0.152	ϕ: β_0	-1.352	0.705
									ϕ: $\beta_{clutchsz}$	-0.249	0.115
									ϕ: β_{RCID}	-0.069	0.020
									p: β_1	-0.044	0.204

clutchsz + RCID + SOI_fall	8	1696.026	1712.065	0.756	0.104	ϕ: β_0	-1.427	0.709
						ϕ: $\beta_{clutchsz}$	-0.234	0.116
						ϕ: β_{RCID}	-0.069	0.020
						ϕ: β_{SOI_fall}	-0.072	0.065
						p: β_1	-0.042	0.204
clutchsz + RCID + fem_recap	8	1696.279	1712.318	1.010	0.092	ϕ: β_0	-1.381	0.706
						ϕ: $\beta_{clutchsz}$	-0.259	0.116
						ϕ: β_{RCID}	-0.066	0.020
						ϕ: $\beta_{fem\ recap}$	0.182	0.182
						p: β_1	-0.044	0.204
clutchsz + CID	7	1698.587	1712.617	1.308	0.079	ϕ: β_0	-1.151	0.743
						ϕ: $\beta_{clutchsz}$	-0.204	0.112
						ϕ: β_{CID}	-0.056	0.017
						p: β_1	-0.041	0.204
clutchsz + RCID + SOI_fall + fem_recap	9	1694.911	1712.960	1.652	0.067	ϕ: β_0	-1.459	0.710
						ϕ: $\beta_{clutchsz}$	-0.244	0.116
						ϕ: β_{RCID}	-0.066	0.020
						ϕ: β_{SOI_fall}	-0.076	0.065
						ϕ: β_{fem_recap}	0.192	0.182
						p: β_1	-0.042	0.204
clutchsz * RCID	8	1697.222	1713.261	1.953	0.057	ϕ: β_0	3.643	8.002
						ϕ: $\beta_{clutchsz}$	0.098	1.383

									ϕ: β_{RCID}	-0.050	0.079
									ϕ:$\beta_{clutchsz*RCID}$	-0.003	0.014
									p: β_1	-0.044	0.204

Table A3.2. *Restricted* data set.

Site	n	No. recruits	Model structure[a]	K[b]	-2logL[c]	AIC_c[d]	ΔAIC_c[e]	ω_i[f]	Parameter[g]	Estimate	SE
SDNRA	9396	464	PDSI * CID + CID_nonlin + mass + fem_recap	11	6225.905	6203.882	0.000	0.769	ϕ: β_0	-3.886	0.571
									ϕ: β_{PDSI}	0.227	0.045
									ϕ: β_{CID}	-0.073	0.021
									ϕ: $\beta_{PDS*CID}$	-0.011	0.005
									ϕ: $\beta_{CID\ nonlin}$	0.002	0.001
									ϕ: β_{mass}	0.071	0.024
									ϕ: β_{fem_recap}	0.228	0.102
									p: β_1	-1.244	0.104
									p: β_2	0.429	0.118
			PDSI + CID + CID_nonlin + mass + fem_recap	10	6229.619	6209.600	3.714	0.120	ϕ: β_0	-3.840	0.569
									ϕ: β_{PDSI}	0.138	0.026
									ϕ: β_{CID}	-0.078	0.021
									ϕ: β_{CID_nonlin}	0.001	0.001
									ϕ: β_{mass}	0.071	0.024
									ϕ: β_{fem_recap}	0.232	0.102
									p: β_1	-1.241	0.104

PG	2934	111	clutchsz + RCID + SOI_fall	8	1395.083	1411.122	0.000	0.162	ϕ: β_0	-1.370	0.768
									ϕ: $\beta_{clutchsz}$	-0.245	0.126
									ϕ: β_{RCID}	-0.074	0.022
									ϕ: β_{SOI_fall}	-0.130	0.077
									p: β_1	-0.199	0.225
			clutchsz + RCID + SOI_fall + fem_recap	9	1393.332	1411.381	0.259	0.142	ϕ: β_0	-1.433	0.770
									ϕ: $\beta_{clutchsz}$	-0.256	0.126
									ϕ: β_{RCID}	-0.069	0.022
									ϕ: β_{SOI_fall}	-0.134	0.077
									ϕ: $\beta_{fem\ recap}$	0.268	0.202
									p: β_1	-0.199	0.225
			clutchsz + RCID	7	1398.111	1412.142	1.020	0.097	ϕ: β_0	-1.243	0.762
									ϕ: $\beta_{clutchsz}$	-0.270	0.125
									ϕ: β_{RCID}	-0.076	0.022
									p: β_1	-0.202	0.225
			clutchsz + RCID + fem_recap	8	1396.536	1412.575	1.453	0.078	ϕ: β_0	-1.304	0.765
									ϕ: $\beta_{clutchsz}$	-0.281	0.125
									ϕ: β_{RCID}	-0.071	0.022
									ϕ: β_{fem_recap}	0.253	0.202
									p: β_1	-0.202	0.225
			clutchsz + CID	7	1398.884	1412.914	1.792	0.066	ϕ: β_0	-1.000	0.802
									ϕ: $\beta_{clutchsz}$	-0.224	0.121

									ϕ: β_{CID}	-0.062	0.018
									p: β_1	-0.200	0.225

Table A3.3. *Highly restricted* data set.

Site	n	No. recruits	Model structure[a]	K[b]	-2logL[c]	AIC$_c$[d]	ΔAIC$_c$[e]	ω$_i$[f]	Parameter[g]	Estimate	SE
SDNRA	8970	432	PDSI * CID + CID_nonlin + mass + fem_recap	11	5788.531	5810.554	0.000	0.759	ϕ: β_0	-3.855	0.591
									ϕ: β_{PDSI}	0.235	0.048
									ϕ: β_{CID}	-0.084	0.022
									ϕ: $\beta_{PDS*CID}$	-0.012	0.005
									ϕ: β_{CID_nonlin}	0.002	0.001
									ϕ: β_{mass}	0.071	0.025
									ϕ: $\beta_{fem\ recap}$	0.196	0.105
									p: β_1	-1.177	0.107
									p: β_2	0.454	0.123
			PDSI + CID + CID_nonlin + mass + fem_recap	10	5794.502	5814.521	3.967	0.104	ϕ: β_0	-3.816	0.590
									ϕ: β_{PDSI}	0.140	0.027
									ϕ: β_{CID}	-0.089	0.022
									ϕ: $\beta_{CID\ nonlin}$	0.0014	0.0006
									ϕ: β_{mass}	0.071	0.025
									ϕ: $\beta_{fem\ recap}$	0.195	0.105
									p: β_1	-1.174	0.107
									p: β_2	0.459	0.123
PG	2515	93	clutchsz + RCID + SOI_fall	8	1164.848	1180.887	0.000	0.193	ϕ: β_0	-0.933	0.822
									ϕ: $\beta_{clutchsz}$	-0.325	0.137
									ϕ: β_{RCID}	-0.083	0.024

						ϕ: β_{SOI_fall}	-0.129	0.085
						p: β_1	-0.111	0.239
clutchsz + RCID	7	1167.275	1181.305	0.418	0.156	ϕ: β_0	-0.783	0.813
						ϕ: $\beta_{clutchsz}$	-0.359	0.134
						ϕ: β_{RCID}	-0.085	0.024
						p: β_1	-0.115	0.239
clutchsz + RCID + SOI_fall + fem_recap	9	1163.576	1181.625	0.738	0.133	ϕ: β_0	-0.982	0.821
						ϕ: $\beta_{clutchsz}$	-0.336	0.136
						ϕ: β_{RCID}	-0.079	0.024
						ϕ: $\beta_{SOI\ fall}$	-0.140	0.086
						ϕ: β_{fem_recap}	0.251	0.222
						p: β_1	-0.112	0.239
clutchsz + RCID + fem_recap	8	1166.396	1182.435	1.548	0.089	ϕ: β_0	-0.819	0.813
						ϕ: $\beta_{clutchsz}$	-0.368	0.135
						ϕ: β_{RCID}	-0.081	0.024
						ϕ: $\beta_{fem\ recap}$	0.207	0.220
						p: β_1	-0.115	0.239
clutchsz + CID	7	1168.427	1182.457	1.570	0.088	ϕ: β_0	-0.576	0.855
						ϕ: $\beta_{clutchsz}$	-0.298	0.131
						ϕ: β_{CID}	-0.068	0.019
						p: β_1	-0.112	0.239

[a] Factors included Palmer Drought Severity Index (PDSI), clutch initiation date (CID), the quadratic term of clutch initiation date (CID_nonlin), relative clutch initiation date (RCID), clutch size (clutchsz), nestling mass (mass), female breeding experience (fem_recap) and SOI August-September (SOI_fall)
[b] Number of estimable parameters.
[c] Deviance.
[d] Akaike's Information Criterion corrected for small sample size.
[e] Difference in AIC_c values between each model and the model with the lowest AICc value.
[f] Estimates of the likelihood of the model, given the data; normalized to sum to 1 (Burnham and Anderson 2002).
[g] Parameter estimates (β) of first-year apparent survival probability (ϕ) and recapture probability (p), including intercepts of first-year apparent survival probability (β_0) and recapture probability for the first-interval (β_1) and second interval (β_2; SDNRA only).